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Regeneration dynamics after fire and clear cutting in boreal mixedwoods

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REGENERATION DYNAMICS AFTER FIRE AND CLEAR CUTTING IN BOREAL MIXEDWOODS

By

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ABSTRACT

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Emulation of natural disturbance processes and their effects is important to maintain the structure and composition of managed forests. In boreal mixed forests, clearcutting has been considered as management practice suitable to mimic stand-replacing fire as both disturbances create conditions of high light availability.

To examine how species with certain regeneration strategy and shade-tolerance respond to different disturbances, a meta-analysis was performed by collecting published data of pre- and post-disturbance stand compositional characteristics in the northern forests. The direct regeneration hypothesis (DRH), which suggests that tree communities will be restored with the same pre-disturbance composition within a few decades after a stand-replacing disturbance (Yih and others, 1991), was tested based on species responses to disturbances. All disturbances promoted broadleaved species regardless of regeneration strategy (suckering, sprouting, or seeding). The DRH was supported by conifers with serotinous cones after fire. Fire caused local extinction of non-serotinous conifers, while wind and clearcutting only decreased the proportion of non-serotinous conifers due to partial survival of seed sources and advance regeneration. The meta-analysis revealed a lack of available data to analyze response of serotinous and semi-serotinous species to clearcutting.

To examine whether logging and fire have different effects on natural regeneration of six common boreal tree species (*Populus tremuloides*, *Betula papyrifera*, *Pinus banksiana*, *Picea mariana*, *P. glauca*, and *Abies balsamea*), density and mean annual height growth of tree regeneration after fire and clearcutting in northern Ontario was studied. Regeneration densities of all studied species, except *P. glauca* and *A. balsamea,* were positively related to their respective pre-disturbance basal area. Post-disturbance regeneration densities and mean annual height growth of *P. tremuloides* and *P. banksiana* did not differ between disturbance types, whereas those of *B. papyrifera* were higher after fire, and those of *P. mariana* and *A. balsamea* were higher after clearcutting. Compared with fire, clearcutting significantly increased the post-disturbance presence of *A. balsamea*, which is attributed to surviving advance regeneration after logging. The natural regeneration process after fire in terms of regeneration density appears to be emulated by clearcutting for *P. tremuloides*, *P. banksiana*, *P. mariana*, and *P. glauca*, but the increase of *B. papyrifera* after clearcutting is less pronounced than after fire, while the reduction of *Abies balsamea* after clearcutting is less severe than after fire. Survival of advance regeneration likely caused higher mean annual growth of *A. balsamea* and *P. mariana*.

The vertical and horizontal structural diversity of live trees was similar following both disturbance types, but species diversity was higher after clearcutting. This increase was attributed to survival of late-successional conifers. All stand-replacing disturbances promote broadleaves, but succession may be accelerated in clearcuts because of the survival of advance regeneration.

Key words: regeneration strategy, shade-tolerance, tree regeneration, fire, clearcutting, boreal mixedwoods

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NOTE TO THE READER

The Chapters 2, 3 and 4 have been submitted for publication as separate manuscripts. Therefore, some overlap in methods, term definitions and presentation of species names may occur. Chapter 2 is in press in Journal of Vegetation Science, Chapter 3 is in press in Ecosystems and Chapter 4 has been submitted to Forest Ecology and Management.

Chapter 2:
Ilisson, T., Chen, H.Y.H. 2009. Direct regeneration hypothesis in northern forests. Journal of Vegetation Science (in press)

Chapter 3:
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Chapter 4:
Ilisson, T. Chen, H.Y.H. 2009. Tree height growth and live tree structural diversity of boreal mixedwoods after fire and clearcutting. Ecosystems (submitted August 2009)

CHAPTER 1. GENERAL INTRODUCTION

The development of boreal mixedwoods and their distribution across the landscape has been historically related to fire regime. Several species have adapted to fire in terms of survival, recovery, and productivity. These species have life history traits that allow individuals or populations to persist on sites after the death of parent trees or tree populations, making them independent of living seed sources from randomly surviving trees in the disturbed area or from forest edges (Rowe, 1983). The most common reproductive traits include vegetative reproduction and cone serotiny. In boreal mixedwoods, species with these regeneration strategies are generally very shade-intolerant, e.g. trembling aspen (*Populus tremuloides* Michx.) or jack pine (*Pinus banksiana* Lamb.). Shade-intolerance, however, is related to a species fast growth rate after the loss of the overstory, giving a competitive advantage over other vegetation for space, light and other environmental resources, resulting in the development of an early-successional tree cohort.

Clearcutting is the most common anthropogenic disturbance in the boreal mixedwoods. It has been widely debated whether clearcutting, if conducted according to the Forest Management Guide of Natural Disturbance Pattern Emulation (Ontario Government, 2002), is suitable for mimicking fire. The proponents of clearcutting state that like fire, clearcutting removes overstory trees creating a high light environment allowing for the development of an early-successional cohort. Opponents, however, refer to several possibly negative influences that differ from fire in the clearcut area and may lead to the development of different stand compositions and lower the overall stand

productivity. The main arguments concerning tree regeneration establishment and growth against clearcutting are:

a) Soil fertility is decreased compared to fire areas, possibly leading to reduced productivity. With stem removal relevant amount of nutrients (especially phosphorous, potassium, calcium and magnesium) are removed. In fire areas, these nutrients are accumulated in the soil. In addition, fire adds charcoal and ash to the soil which increase soil pH. In more alkaline soils, nutrient binding and water movement are increased (McRae and others, 2001).

b) The quality of seed beds in the clearcuts may be lower than those in the fire areas. The rule of thumb is that in the upland forests, seed bed suitability for establishment, germination and early survival of seedlings is positively related to lower organic layer depth (Nguyen-Xuan and others, 2000; McRae and others, 2001; Calogeropoulos and others, 2004). In burns, the organic material is often either entirely or partially consumed by flames, while in clearcuts, the organic layer is generally decreased only on patchy areas due to machinery movement.

c) In clearcuts, there is a lack of heat necessary for seed release from serotinous cones. Serotinous cones open when temperatures exceed 50^0C (Farmer, 1997). There is concern that in the clearcuts, the regeneration of serotinous species may be endangered unless planting or seeding is done.

d) Soil compaction due to forest machinery movement may inhibit plant establishment and growth for both asexually and sexually reproducing species (McRae and others, 2001).

Several studies have examined the response of boreal tree species to fire (Greene and Johnson, 1999; Lepage and others, 2000; Greene and others, 2004; Chen and others, 2009). Most studies confirm that post-disturbance regeneration density and species composition are positively related to the species specific basal area in the stand prior to disturbance. For vegetatively reproducing species, the relationship reflects the size of the bud bank capable of supporting regeneration; and for serotinous species, the pre-disturbance basal area is related to the seed supply in the tree canopies. Therefore, pre-disturbance composition should be considered when studying regeneration dynamics. However, it remains unclear to what extent the relationship applies to clearcutting.

The purpose of this thesis was to compare regeneration development between fire and clearcutting areas. First (Chapter 2), we wanted to clarify what kind of species specific life-history traits and to what extent these traits influence compositional development after stand replacing disturbances. We chose three types of common disturbances in northern forests (fire, wind and clearcutting) to find out whether the response of species is due to specific disturbance effects or life traits. Besides demonstrating the major importance of vegetative reproduction ability (it generally always secures the success of species after stand-replacing disturbances), several gaps in the present knowledge about regeneration dynamics revealed. Specifically, we found that the understanding of compositional development in relation to pre-disturbance

composition should be improved as there are species specific differences in vegetative reproduction and seeding rates. We also identified a lack of information concerning the response of serotinous and semi-serotinous species to clearcutting disturbance.

To get a better understating of these uncertainties, two field studies were performed (Chapter 3 and 4). We studied the regeneration development of boreal mixedwoods composed by six common tree species (trembling aspen, paper birch (*Betula papyrifera* Marsh.), jack pine, black spruce (*Picea mariana* (Mill.) B.S.P.), white spruce (*P. glauca* (Moench) Voss), and balsam fir (*Abies balsamea* (L.) Mill.) in varying proportions after fire and clearcutting. Specifically, we wanted to (1) know the extent to which species regeneration density and its relative proportions in the stand are related to pre-disturbance stand composition, and whether this relationship differs between fire and clearcutting (Chapter 3), and (2) compare mean annual tree height growth and live tree structural diversity in fire and clearcutting areas (Chapter 4). Height growth and live tree structural diversity reflect changes in a site's productivity and indicate the possibility of mechanical damage to soil caused by forest machinery.

CHAPTER 2. THE DIRECT REGENERATION HYPOTHESIS IN NORTHERN FORESTS

INTRODUCTION

The direct regeneration hypothesis (DRH) states that tree communities will be restored with the same pre-disturbance composition within a few decades after a stand-replacing disturbance (Yih and others, 1991). The hypothesis is used to predict vegetation responses after stand-replacing windthrow in tropical forests (e.g. Yih and others, 1991; Basnet, 1993; Boucher and others, 1994; Bellingham and others, 1995; Vandermeer and others, 1995; Baldwin and others, 2001; Batista and Platt, 2003) and after fires in Mediterranean and Chaparral fire-prone ecosystems (e.g. Tarrega and others, 1997; Odion and Davis, 2000; Franklin and others, 2001; Rodrigo and others, 2004; Arnan and others, 2007). The main reason for direct regeneration is the component species' disturbance adaptations that can be expressed by the proportionality of basal area of parent tree population to its seed production, seed dispersal, or vegetative reproduction capability. The relationship between a stand's pre-and post-disturbance basal area or density has been demonstrated by a number of studies in northern forests (Lavoie and Sirois, 1998; Greene and Johnson, 1999; Wang, 2003; Greene and others, 2004; Johnstone and others, 2004; Johnstone and Chapin, 2006; Chen and others, 2009) making it possible to test the applicability of the hypothesis at a broad scale after three common stand-replacing disturbances – fire, windthrow, and clearcutting.

Tree species may respond differently to fire, windthrow, and clearcutting disturbances because of their effects on substrate creation, microclimate, and propagule availability (Roe and others, 1970; Nguyen-Xuan and others, 2000; Elson and others, 2007). Unlike fire, clearcutting and windthrow remove little of the soil organic layers (Prevost and Pothier, 2003), which may lead to development of residual vegetation (Haeussler and others, 2002) instead of a newly established cohort by seeds or sprouts. Following wind disturbance, heterogeneous micro-relief is created due to uprooting of trees (Greenberg and Mcnab, 1998; Ulanova, 2000), creating shaded soil pits with exposed mineral soil (Peterson and Pickett, 1995), while on undamaged forest floor advance regeneration may survive (Dyer and Baird, 1997; Peterson, 2000). Disturbance type is, therefore, likely to have an effect on vegetative reproduction ability, cone serotiny, development of advance regeneration, and growth rate at the regeneration stage. The last can be characterized by species shade-tolerance at the regeneration stage (Burns and Honkala, 1990; Chen and others, 1996b).

Vegetative reproduction and cone serotiny are adaptation strategies to fire and wind disturbances in northern forests. Vegetative reproduction is common to all hardwoods in northern forests, allowing individuals to persist on the site and possessing a growth advantage compared to seedlings, owing to carbohydrate supplies provided by root systems of killed or damaged parent trees (Bond and Midgley, 2001; Del Tredici, 2001). Stem sprouting and root suckering have been found to be promoted by fire, logging, and wind disturbances (Del Tredici, 2001) as these disturbances eliminate apical dominance and increase light levels after overstory removal. Cone serotiny, on

the other hand, allows species to store seeds in an aerial seed bank and disperse seed shortly after fire when suitable seed bed conditions are created, destruction of understory vegetation and exposure of mineral soil (Nguyen-Xuan and others, 2000). In clearcuts and windthrow areas, cone serotiny may not be advantageous because of the lack of heat required for cone opening. Although some studies have reported cone opening in clearcuts due to increased temperatures on sun exposed mineral soil (Chrosciewicz, 1960), the distribution of cones from logging residues should result in a smaller seed dispersal radius compared to the dispersal from the canopies of standing fire-killed trees.

While regeneration strategy determines the extent to which species are capable of re-establishment, shade-tolerance can be an important predictor of success in post-disturbance communities (Pausas and Lavorel, 2003; Pausas and Verdu, 2005). In many disturbed ecosystems, shade intolerance of a species is associated with rapid growth under full light availability in newly disturbed areas (Chen, 1997; Chen and Klinka, 1997). Rapid initial growth provides a competitive advantage over other vegetation (Haeussler and others, 2004; MacDonald and others, 2004; Bond-Lamberty and others, 2007; Chen and others, 2009). Shade tolerance is a good indicator of a species' ability to withstand competition under a closed canopy with morphological and physiological traits such as a high specific leaf area, large seeds, rapid expansion of deep roots, and a low photosynthetic compensation point (Chen, 1997; Chen and Klinka, 1997; Reich and others, 1998). These species may play an important role as advance regeneration or as

seed sources after wind or clearcutting disturbance. Coupled with regeneration strategy, shade tolerance may determine a species' response to disturbances.

In this study, we test if DHR is suitable for predicting post-disturbance regeneration by investigating the relationships between pre- and post-disturbance stand compositions following stand-replacing fire, windthrow, and clearcutting of the northern forests of North America. We expect that species with different life traits respond differently to fire, windthrow, and clearcutting due to varying effects of these disturbances on environment, microclimate and propagule availability. To facilitate testing the DRH, we use compositional difference (CD), i.e., percentage of basal area of the post-disturbed stand subtracted from that of the pre-disturbance stand. DRH is supported when CD is 0.

Specifically, we hypothesize that DRH will be (i) rejected for broadleaves with strong vegetative reproduction ability because sprouting or suckering allows rapid establishment after disturbance, enables domination over other species, and as a result an increase in species proportion, (ii) accepted for broadleaves that regenerate mainly by seeds after windthrow and clearcutting attributed to partial survival of seed sources, and after fire because of the creation of suitable seed beds (burned organic layers and exposed mineral soil), (iii) accepted for serotinous and semi-serotinous conifers after fire because of the aerial seed bank and the heat that allows seed release, but rejected after clearcutting due to the absence of a seed bank and heat, (iv) rejected for non-serotinous conifers after fire because of the elimination of seed sources and advance regeneration, but accepted after wind and clearcutting because of partial survival of

seed sources and advance regeneration. Furthermore, we expect a species' shade tolerance, although coupled with regeneration strategy, may help explain additional variations of regeneration success in response to different disturbances. For example, shade-tolerant species may be better maintained after clearcutting and windthrow than fire because of partial survival of advance regeneration.

METHODS

SYNTHESIS APPROACH

We selected post-disturbance regeneration studies with the pre-disturbance stand composition given either used in analyses (e.g.Arevalo and others, 2000; Bergeron, 2000; Greene and others, 2004) or in study area description (e.g.Walker and Johnson, 1975; Cooper-Ellis and others, 1999), resulting in 21 studies (Appendix 1). Species composition (%) was determined using basal area for both pre- and post-disturbance data, but the composition of stands younger than 25 years was determined using stem density since most stems in young stands were too small for basal area measurement. Since high initial densities of species can lead to its dominance and consequently suppress other species, we assume the proportions of stem density at the early stage would mirror the basal area proportions at the later stage of stand development. In order to minimize the effects of succession, only post-disturbance stands up to 50 years after disturbance were included in the analysis. Compositional difference (CD) was calculated as the difference between post-disturbance relative basal area or density and pre-disturbance relative basal area.

We included only studies that reported both pre- and post-disturbance compositions of the same stand. The data from single study plot inside one stand was considered as one observation. When multiple plots were established in one stand, the mean of these plots was considered as one observation. When there were data from repeated regeneration surveys in the same area, only the latest observations (up to 50 years since disturbance) were included. When data was presented in figures, the SigmaScan Software (SPSS Inc., 1999) was used to extract the individual data points. Data from stands receiving silvicultural treatments following disturbance were not included. Because there were a limited number of studies for analysis, we used an unweighted meta-analysis as previously recommended (Osburn and Callender, 1992; Clark and others, 1999; Johnson and Curtis, 2001; Knorr and others, 2005).

Table 2. 1 Studied species and their grouping by regeneration strategy and shade tolerance

Regeneration strategy	Shade-tolerance	Species
Broadleaves with strong vegetative reproduction ability	Intolerant	*Betula papyrifera (Bep), Populus balsamifera (Pob), Populus grandidentata (Pog), Populus tremuloides (Pot), Prunus serotina (Prs), Quercus ellipsoidalis (Que)*
	Intermediate	*A. rubrum (Acr), Caraya spp (Cas), Quercus alba (Qua), Q. macrocarpa (Qum), Q. rubra (Qur)*
	Tolerant	*Acer negundo (Acn), Acer saccharum (Acs), Fagus grandifolia (Fag), Ostrya virginiana (Osv)*
Broadleaves with weak vegetative reproduction ability	Intolerant	*Betula lenta (Bel), Betula nigra (Ben), Fraxinus nigra (Frn), Prunus pennsylvanica (Prp)*
	Intermediate	*Betula alleghaniensis (Bea), Fraxinus americana (Fra), Ulmus americana (Ula)*
	Tolerant	*Ulmus rubra (Ulr), Tilia americana (Tia)*
Conifers with serotinous cones	Intolerant	*Pinus banksiana (Pib), Pinus contorta (Pic)*
Conifers with semi-serotinous cones	Intermediate	*Picea mariana(Pim)*
Conifers without serotinous cones	Intolerant	*Larix laricina (Lal), Pinus resinosa (Pir)*
	Intermediate	*Picea glauca (Pig), Pinus strobes (Pis)*
	Tolerant	*Abies balsamea (Abb), Tsuga canadensis (Tsc), Thuja occidentalis (Tho)*

Species were classified by regeneration strategy and shade-tolerance according to Burns and Honkala (1990) and Hewitt (1998). Regeneration strategy classes were: broadleaves with strong vegetative reproduction ability (SV-B), broadleaves with weak vegetative reproduction ability (WV-B), conifers with serotinous cones (S-C), conifers with semi-serotinous cones (SS-C), and conifers with non-serotinous cones (W). Shade-tolerance was classified as intolerant, intermediate, and tolerant species (Table 2.1). Vegetative species were divided into strong and weak groups based on their prevailing response to severe disturbances. If regeneration of a species was primarily asexual, the species was classified as a strong vegetative reproducer. When reproduction by seed dispersal was more prevalent, a species was classified as a weak vegetative reproducer.

DATA ANALYSIS

To examine the effect of disturbance and life traits on CD, we performed three analyses. First, we tested disturbance type and regeneration strategy, and their 2-way interactions on CD. Second, because regeneration strategy and shade tolerance are coupled, i.e., species with strong vegetative reproduction are shade intolerant, we tested whether CD was affected by shade tolerance and disturbance. Lastly, we added shade tolerance into the first model to examine whether added variation of CD could be explained by including disturbance, regeneration strategy, and shade tolerance. We performed two-tailed Student's T-tests to further examine whether CDs of individual functional groups were significantly different from zero. Tests were considered relevant when they have at least 80% power with medium or large effect size (Cohen, 1988; Cohen, 1992). Power analyses were performed using the program G*Power version 3

(Faul and others, 2007). All other statistical analyses were performed using SPSS 15.0 (SPSS Inc., 2006).

RESULTS

When tested using disturbance, regeneration strategy, and their interaction as explanatory variables, CD was significantly affected by regeneration strategy, but not by disturbance and the interaction of disturbance and regeneration strategy (Table 2.2, and Figure 2.1). The model explained 14.7% of the variation of CD, mostly attributed to regeneration strategy. When CD was tested using disturbance and shade tolerance as predictors, shade tolerance was significant, but the model explained less variation of CD than the regeneration strategy model (Table 2.2). When all three factors were included as predictors, regeneration strategy was the only significant factor, suggesting a coupled effect of regeneration strategy and shade tolerance.

Among five regeneration strategy groups, broadleaves with strong vegetative reproduction had significantly higher CDs (mean CD = 7.95%) than conifers with serotinous, non-serotinous and semi-serotinous cones (mean CD = -0.18% and P = 0.045, -8.83% and <.0001, -11.75% and <.0001, respectively). Broadleaves with weak vegetative reproduction had higher CD (mean CD= 7.53%) than conifers without serotinous and semi-serotinous cones (mean CD = -8.83% and P = 0.041, -11.75% and P = 0.007, respectively).

Table 2. 2 Effects of disturbance type, regeneration strategy, and shade-tolerance on compositional difference (CD, %).

Source	df	MS	F	P	Partial Eta^2
Model 1	10	2411.8	5.21	<0.001	0.147
Intercept	1	549.6	1.19	0.277	0.004
Disturbance (D)	2	651.4	1.41	0.247	0.009
Regeneration Strategy (RS)	4	4427.5	9.56	<0.001	0.112
D x RS	4	186.1	0.40	0.807	0.005
Error	302	463.1			
Model 2	9	1353.0	2.71	0.005	0.074
Disturbance (D)	2	231.8	0.46	0.629	0.003
Shade Tolerance (ST)	2	2146.3	4.29	0.014	0.027
D x ST	4	450.4	0.90	0.464	0.012
Error	304	499.8			
Model 3	23	1168.8	2.46	<0.001	0.164
Intercept	1	215.5	0.45	0.501	0.002
Disturbance (D)	2	785.0	1.65	0.193	0.011
Regeneration Strategy (RS)	4	2395.4	5.05	0.001	0.065
Shade Tolerance (ST)	2	23.7	0.05	0.951	0.001
D x RS	4	232.1	0.49	0.744	0.007
D x ST	4	176.9	0.37	0.828	0.005
RS x ST	4	96.3	0.20	0.937	0.003
D x RS x ST	3	90.1	0.19	0.903	0.002
Error	289	474.4			

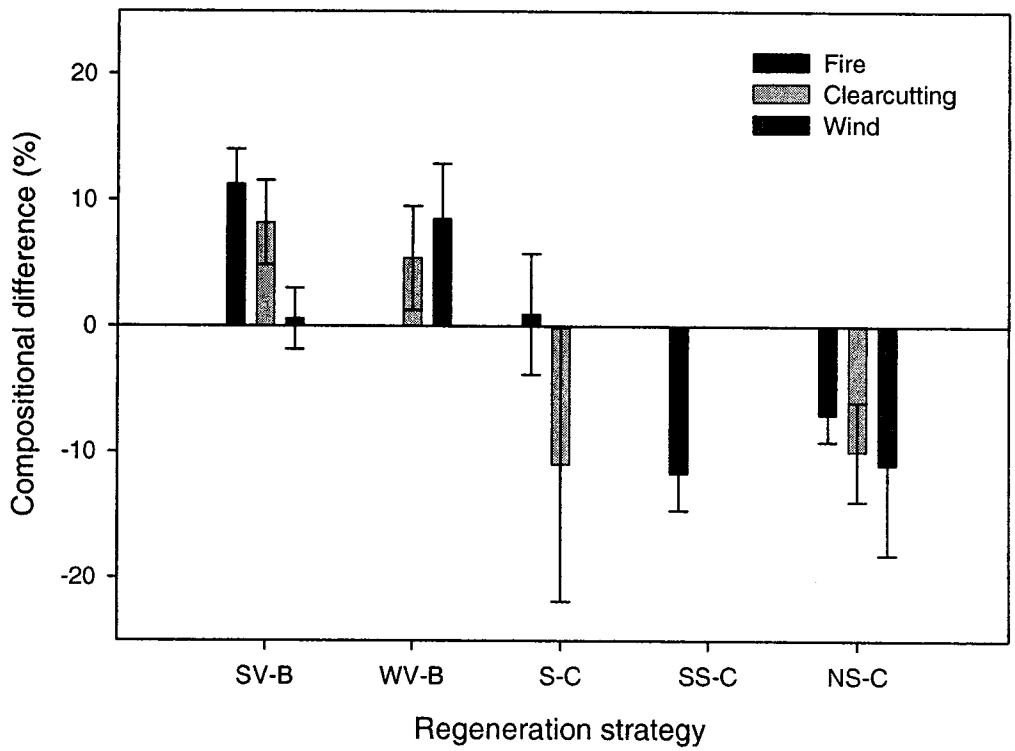

Figure 2. 1 Species compositional difference between post- and pre-disturbance stands (CD, %) by regeneration strategy after fire, clearcutting and windthrow (mean ± 1 se). Regeneration strategy groups: broadleaves with strong vegetative reproduction (SV-B), broadleaves with weak vegetative reproduction (WV-B), conifers with serotinous cones (S-C), conifers with semi-serotinous cones (SS-C), and conifers without serotinous cones (NS-C). Missing bars represent unavailability of data.

Both groups of broadleaves (with strong and weak vegetative reproduction ability) responded to all disturbances as hypothesized with significantly positive CD values. Conifers with serotinous cones had mean CD not significantly different from zero, while the CD of conifers with semi-serotinous cones was smaller than zero. Conifers with non-serotinous cones had significantly negative CD values (Table 2.3).

Table 2. 3 Results from 2-tailed Student's *t* of the hypothesis compositional difference (CD, %) = 0. Individual regeneration strategy group is analyzed separately regardless disturbance. Regeneration strategy groups: broadleaves with strong vegetative reproduction (SV-B), broadleaves with weak vegetative reproduction (WV-B), conifers with serotinous cones (S-C), conifers with semi-serotinous cones (SS-C), and conifers without serotinous cones (NS-C). [a]Power with effect size 0.5 is marked with * and with effect size 0.8 with **.

Regeneration strategy	*t*	df	*P*	Mean CD (%)	Effect size	Power[a]
SV-B	4.51	142	<0.001	7.95	0.4	0.99*
WV-B	2.34	18	0.031	7.53	0.8	0.91**
S-C	0.04	45	0.971	0.17	0.5	0.91*
SS-C	-4.01	47	<0,001	-11.75	0.5	0.92*
NS-C	-4.15	56	<0.001	-8.83	0.5	0.96*

DISCUSSION

The direct regeneration hypothesis (DRH) predicts that following disturbance, species proportions will remain similar to those prior to disturbance, in ecosystems prone to stand-replacing disturbances, assuming that all component species can equally occupy growing space available after the disturbance, depending on only pre-disturbance species-specific stand basal area, a surrogate for propogule availability after the disturbance (Yih *and others*, 1991; Vandermeer *and others*, 1995; Rodrigo *and others*, 2004). The results of our study demonstrate that the DRH can predict postfire species proportions for conifers with serotinous cones. Other functional groups, however, either increased or decreased in their proportions.

Fire, clearcutting, and windthrow increased the proportion of vegetatively reproducing broadleaves. This result was expected as these disturbances kill parent trees and eliminate apical dominance (Del Tredici, 2001). High belowground carbohydrate storage allows fast development of basal sprouts, trunk sprouts and/or root suckers after stem removal, providing an advantage over species that reproduce by seeds (Heinselman, 1981; Bond and Midgley, 2001). In addition, some advance regeneration can survive windthrow and clearcutting. For example, *Acer* spp, *Tilia* spp and *Fagus* spp are known to form an understory tree layer under mature canopies. After windthrow or clearcutting, the understory layer of advance regeneration becomes a significant component of the post-disturbance stand (Bormann and Likens, 1979; White, 1991; Collet and others, 2008).

Similar to species with strong vegetative ability, the broadleaves that reproduce mainly by seeds increased after windthrow and clearcutting. In clearcuts and wind disturbed areas, seed sources remain available and both disturbances create varying microrelief with random patches of exposed mineral soil. These patches efficiently contribute to the establishment of seeds of broadleaf species (Peterson and others, 1990; Bazzaz, 1996; Peterson and Pickett, 2000). However, no data were available for postfire areas. After fire, lower seed dispersal, due to the elimination of seed sources, could be compensated by the large amount of suitable seed beds (Nguyen-Xuan and others, 2000) and subsequent rapid growth, resulting in increased proportions.

For serotinous tree species, fire-induced high temperatures create suitable seedbeds and stimulate cones to release seeds (Johnson and Gutsell, 1993; Lamont and

Enright, 2000). Therefore, it was expected that the presence of serotinous species after fire is highly correlated to seed source, predicted from stand basal area. Semi-serotinous species, i.e., *Picea mariana*, however, in spite of fire-adaptation, decreased after fire. Possible explanations to negative CD values include destroyed aerial seed bank because of very high fire intensity (Arseneault, 2001), young age of the pre-disturbance stand (low stored seed bank), unsuitable seedbed conditions before and after fire (Foster, 1985; Lavoie and Sirois, 1998), post-fire seedling suppression by more fast growing species e.g., *Populus* spp. (Johnstone and others, 2004), and a longer period of regeneration process and slower initial height growth than its associated species (Vasiliauskas and Chen, 2002; Chen and Wang, 2006). Despite its fire adaptation, black spruce has been found to act as a late-successional species on upland sites, increasing its proportion through stand development (Harper and others, 2002).

The paucity of data did not allow analyzing responses of serotinous and semi-serotinous species after clearcutting. Only two studies including both pre- and post-disturbance data for species with serotinous cones (Hughes, 1967; Walker and Johnson, 1975) and no studies with data of semi-serotinous species after clearcutting were found. It is generally recognized that clearcutting without silvicultural treatments has a negative influence on the regeneration of serotinous and semi-serotinous species (Nelson, 1977; Brumelis and Carleton, 1988; Frelich and Reich, 1995), but the dependence on pre-clearcutting proportion, however, remains to be clarified.

The proportion of non-serotinous conifers decreased significantly after all disturbances. However, the difference in disturbance effect between fire and other

studies was the disappearance of non-serotinous conifers in all 26 post-fire cases, while clearcutting resulted in extirpation of only six cases out of 21 and wind caused extirpartion in two cases out of ten. There are two possible explanations. First, fire removes most or all of the seed sources (Timoney and Peterson, 1996; Eastham and Jull, 1999; Lepage and others, 2000), while in clearcuts, trees of low commercial value left standing may act as seed sources. Similarly, several studies from windthrow stands report some survival (Webb, 1989; Peterson and Pickett, 1995; Dyer and Baird, 1997; Arevalo and others, 2000; Peterson, 2000; Ulanova, 2000). However, seed establishment should be poor in clearcuts and wind disturbed areas due to poor seedbed quality of organic layers (Eastham and Jull, 1999; Prevost and Pothier, 2003) and competition with surviving and developing vegetation for light, nutrients and water (Berkowitz and others, 1995; Prevost and Pothier, 2003). Secondly, the influence of fire, wind and clearcutting on advance regeneration is very different. Fire destroys understory vegetation, while in clearcut and wind disturbed areas, some survival may occur. In clearcuts, the rate of survival depends on harvesting methods, equipment, and time of year. Different studies report both survival (Carleton and MacLellan, 1994; Harvey and Brais, 2002) and severe damage (Timoney and Peterson, 1996). In our analysis these explanations are supported by three studies from burn areas that report lack of residual trees in study plots at least 100 meters away from the residual edges (Ohmann and Grigal, 1979; Charron and Greene, 2002; Chen and others, 2009), by two studies that report severe crown fires (Heinselman, 1981; Greene and others, 2004), likely meaning that all canopy trees were killed and by three studies reporting survival of advance

regeneration in clearcuts (Marquis, 1967; Walker and Johnson, 1975; McInnis and Roberts, 1994).

Shade-tolerance did not explain any variation of CD in addition to regeneration strategy. When analyzed with shade tolerance and disturbance as predictors, shade tolerance was significant, indicating the coupling of regeneration strategy and shade tolerance. For example, Shade intolerant species, mostly with strong vegetative reproduction, are typically promoted by fire and clearcutting (Wang, 2003; Greene and others, 2004).

It is somewhat puzzling that responses within regeneration strategy or shade-tolerance groups did not differ among disturbance types. The lack of disturbance effect among strong vegetative reproducers is due to the fact that all studied disturbances kill the main stem during very short periods (as opposed to slow weakening by the disease or insect attack) (Heinselman, 1981; Bond and Midgley, 2001), which allows fast sprouting and sufficient support of saplings with nutrients from the root systems. It is possible that vegetative reproduction ability has the highest importance in development of species composition after stand-replacing disturbances outweighing effects of seed supply and seed bed availability, germination conditions or even a species' shade-preferences in early growth stage. Vegetative reproduction allows persistence of individuals on a site in the form of suckers or sprouts, eliminating the "time-consuming" establishment and germination phase. Persistence of established trees reduces recruitment opportunities in space and time for seed dispersed species (Bond and Midgley, 2001) possibly explaining increased proportions of sprouters and suckers, and

decreased proportions of non-serotinous conifers after all disturbances. An example of importance of vegetative reproduction rather than seed dispersal or shade-tolerance is given by Schulze *et al.* (2005) who found that in the Siberian dark taiga, the very shade-tolerant conifer *Abies sibirica* became dominant after windthrow due to strong layering ability, outcompeting shade-intolerant seed dispersed broadleaves that are otherwise commonly found dominating on disturbance sites. It remains to be clarified whether the lack of disturbance effect among non-serotinous conifers was because of pre-occupied space by suckers and sprouters or due to specific disturbance effects on seed limitation and establishment or germination conditions.

The increase of broadleaves at the expense of non-serotinous conifers following stand replacing disturbances may have profound implications on the future composition of the northern forests if the frequency of disturbances such as fire increase in association with changes in climate and atmospheric carbon dioxide concentration (Bond-Lamberty and others, 2007). Succession may increase the relative abundance of non-serotinous conifers as stand ages without a stand replacing disturbance (Bergeron, 2000; Chen and Popadiouk, 2002). Increased disturbance frequencies, i.e., shorter disturbance return intervals, will limit non-serotinous conifers recruitments that are associated with canopy gaps at late stages of stand development (Kneeshaw and Bergeron, 1998; Hill and others, 2009). Consequently, the composition of broadleaves may increase in the future if disturbance frequencies are to increase as predicted (Bond-Lamberty and others, 2007).

CONCLUSIONS

The DRH can predict post-fire species proportions for conifers with serotinous cones. Other functional groups showed either increased or decreased proportions. All disturbances increase the proportion of all broadleaf species. Species with vegetative reproduction ability are promoted as all of the disturbances kill overstory trees, eliminating apical dominance and advancing the development of sprouts and suckers supported by nutrients in the parent tree root systems. Seed establishment of broadleaves is either supported by creation of large numbers of suitable seed beds (fire areas) or partially survived seed source (wind and clearcutting disturbed areas). Fire causes local extinction of non-serotinous conifers, while clearcutting and wind disturbances only decrease their proportion. The difference is due to the survival of advance regeneration in clearcuts and wind disturbed areas or to seeds from surviving trees. A species' regeneration strategy can be used to predict their response to stand-replacing fire, clearcutting or windthrow disturbances in boreal and northern temperate forests. Shade-tolerance has only a minor additional effect.

Results of this study combined with the literature suggest that a species' ability to regenerate vegetatively enables domination over species with other regeneration strategies because it allows a species' persistence and limits recruitment opportunities for species depending on sexual reproduction. Investigation of mixtures where species with different regeneration strategies coexist is needed to verify which traits dominate in development of post-disturbance composition. Questions to be addressed are: (i) Is the development of post-disturbance composition influenced by the presence of strong

vegetative reproducers rather by the specific disturbance effects on microenvironment and propagule availability? In other words, in the mixed species stands, does the proportion of species with other regeneration strategies (e.g., seeds from serotinous or semi-serotinous cones, light long-dispersed seeds of broadleaves or heavier non-serotinous seeds of conifers) decrease because of pre-occupied space by sprouters and suckers? (ii) In the absence of strong vegetative reproducers, what determines the development of composition? Is it the presence of species with next most aggressive regeneration strategy (e.g., light wind-dispersed seeds), specific disturbance effects or combination of both of these? In addition, the unavailability of data suggests that the response of serotinous and semi-serotinous species to the clearcutting needs to be clarified.

CHAPTER 3. RESPONSE OF SIX BOREAL TREE SPECIES TO STAND REPLACING FIRE AND CLEARCUTTING

INTRODUCTION

Emulation of natural disturbance processes and effects is considered central to sustainable forest management (Hunter, 1999). Along with the worldwide trend driven by the need for natural resources (Foley and others, 2005), forest harvesting, mostly mechanical clearcutting, takes place in the boreal forest with approximately 900,000 ha cut per year in Canada (Canadian Council of Forest Ministers (CCFM), 2005). The boreal forest successfully regenerates naturally after fire. Similarly, natural regeneration is also the most common regeneration method after clearcutting, accounting for approximately 85% of successfully regenerated land (Canadian Council of Forest Ministers (CCFM), 2005). However, the extent to which natural regeneration processes after clearcutting emulates that after fire is unclear.

Postfire natural regeneration can be predicted based on prefire species composition. For most shade-intolerant boreal tree species, postfire regeneration densities are positively related to their prefire stand basal area (Greene and Johnson, 1999; Greene and others, 2004; Chen and others, 2009), indicating the importance of propagule availability on postfire natural regeneration. In addition, postfire regeneration tends to vary with fire severity, that affects microclimate, substrate, competition, and propagule availability for natural regeneration (Wang, 2003; Greene and others, 2004; Johnstone and Kasischke, 2005; Greene and others, 2007). Although natural

regeneration after logging has been less studied, advance regeneration has been shown to be a significant component of post-harvest stands (Greene and others, 2002; Harvey and Brais, 2002).

Fire and mechanical clearcutting are two distinct processes, one killing trees by fire induced high heat, and the other physically removing living trees (McRae and others, 2001), resulting in different regeneration substrates, coarse woody debris structures, and understory vegetation communities (Brassard and Chen, 2008; Hart and Chen, 2008). In this study, we attempted to examine natural regeneration responses of six boreal tree species (*Populus tremuloides* Michx., *Betula papyrifera* Marsh., *Pinus banksiana* Lamb., *Picea mariana* (Mill.) B.S.P., *P. glauca* (Moench) Voss, and *Abies balsamea* (L.) Mill.) to fire and clearcutting. We hypothesize that natural regeneration differs after fire and clearcutting. First, we expect both *P. tremuloides* and *B. papyrifera* to increase after fire and clearcutting since stand replacing disturbances tend to favor species that reproduce vegetatively (Pausas and others, 2004; Rodrigo and others, 2004; Chen and others, 2009). Second, because fire creates a heating effect to promote seed dispersal for species with serotinous cones and reduces depth of forest floor to create more suitable seedbeds in the form of thin humus or mineral soil (Nguyen-Xuan and others, 2000), we expect regeneration of *P. banksiana* and *P. mariana* would be better promoted after fire than clearcutting. Third, we predict that late-successional species *P. glauca* and *A. balsamea* will decrease in post-disturbance stands, but will be more favored after clearcutting than fire, since some of the advance regeneration of these

species in the boreal mixedwood stands can survive clearcutting, but not fire (Chen and Popadiouk, 2002; Greene and others, 2002).

METHODS

STUDY AREA

We sampled both post-fire and post-clearcutting sites in the boreal mixedwood in northwestern Ontario Spruce River Forest and the Black Sturgeon Forest. The study area is in the boreal forest north of Lake Superior and west of Lake Nipigon in the Upper English River (B.11) Forest Regions (Rowe, 1972), approximately 150 km north of Thunder Bay, Ontario (48° 22' N, 89° 19' W, 199 m elevation). The study area has a moderately dry, cool climate with short summers. The average annual precipitation for Thunder Bay (1971-2000) is 712 mm and the average annual temperature is 2.5 °C (Environment Canada, 2007). The area belongs to the moist mid-boreal ecoclimatic region (Ecoregions Working Group (EWG), 1989). The topographic features were shaped by the retreat of the Laurentide Ice Sheet approximately ten millennia ago, resulting in rolling topography.

The region is part of the boreal mixedwood forest, with upland forests consisting primarily of mixtures of *P. tremuloides*, *B. papyrifera*, *P. banksiana*, *P. mariana*, *P. glauca*, and *A. balsamea* with a small contribution from red pine (*Pinus resinosa* Ait), white pine (*Pinus strobus* L.), tamarack (*Larix laricina* (Du Roi) K. Koch), and Eastern white cedar (*Thuja occidentalis* L.) on some sites (Rowe 1972). Fire is the most common natural stand-replacing disturbance in the study area. The last spruce budworm

(*Choristoneura fumiferana* Clem.) epidemic peaked in 1986 and collapsed approximately 10 years later (Paul Poschmann, personal communication), causing significant mortality of host-specific trees (i.e., *A. balsamea* and *Picea* spp.).

FIELD MEASUREMENTS

Field data collection took place in summer 2007. To facilitate sampling, a wide range of pre-disturbance stand composition sample areas were selected using forest inventory maps. Pre-disturbance stand ages ranged from 80 to 150 years. Since most natural regeneration processes of boreal tree species are completed within five years after fire and clearcutting (Lavoie and Sirois 1998; Gutsell and Johnson 2002; Johnstone and others 2004), we selected both postfire and post-clearcutting stands approximately 5 to 15 years after the stand replacing disturbance, similar to Chen *et al.* (2009).

It is difficult to have a well-balanced design to study the effects of natural disturbances (Turner and others, 1997; Parker and Wiens, 2005). In the study area, there was one large fire that occurred during the decade of interest (1992-2002), which took place on April 30, 1998, and burnt 26,400 ha of various stand types and site conditions. We used *post facto* and before-after control-impact designs recommended by Parker and Wiens (2005). Post-clearcutting stand ages ranged from 6 to 12 years from operations occurring from 1995 to 2001. All sites were harvested in the whole tree harvesting method – trees were cut and then cleaned from branches on the signed lot or by the roadside. Harvesting took place in the winter or early spring seasons. All selected fire sites were left to regenerate naturally without salvage logging or other treatments. To minimize the possibility of seeds from undisturbed areas, the plots were established a

minimum of 250 meters from unburned or uncut forest edges. To avoid any potential spatial influence from neighboring sample plots, all plots were allocated approximately > 50 m apart (most of them over 200 m). To minimize the influence of silviculture on natural regeneration, we did not select any sites that had received site preparation, seeding, or vegetation management. However, because of limited availability of untreated *P. banksiana* dominated stands, which typically receive seeding or planting treatment in the study area, we included several sites that did not receive any other silvicultural treatments except spot planting, but planted trees were excluded from analyses.

For each of the six study species and each disturbance origin, we attempted to sample at least five replicates of each of the four pre-disturbance composition groups (< 25, 25-50, 51-75, and > 75%) based on relative basal area of each species in a sample stand, which was used to facilitate sampling design, but actual species compositions were used in the analysis. In total, we sampled 56 postfire stands and 47 post-clearcut stands. Every effort was made to intersperse stands to avoid sampling stands in close proximity to one another in order to minimize the impact of spatial structure (Legendre and Legendre, 1998). To limit site variability, all sites were located on flat, mid slope positions, with no slope exceeding 5%, on well-drained glacial moraines greater than 50 cm in thickness. This is the prevailing site type in the region. In the field, site condition was determined by topographic characteristics and soil profile determined from a soil pit dug randomly in each sampled stand.

On each selected site, pre-disturbance stand structure and composition was determined by a 20 x 20 m plot. Within the plot, only live trees at the time of the fire or logging were measured. Dead trees that had been killed by fire or logging still have solid structure after 5 to 15 years. Tree species were identified based on bark recognition, mode of regeneration, and architecture, as described in Chen and others (2009). We measured breast-height diameters (1.3 m) in the post-fire stands and root-collar diameters on stumps in clearcut stands. To calculate breast height diameter for trees in clearcuts, models of root-collar to breast-height diameter relationships for each of six tree species were created by collecting data from surrounding intact stands. For each species, one hundred trees of variable sizes were randomly selected for diameter measurements.

Post-disturbance regeneration was assessed in three randomly located 5 x 5 m sub-plots in the 20 x 20 m plot that was used to determine the pre-disturbance stand condition. All regenerating tree species were identified and trees were counted in the subplots.

ANALYSIS

When analyzing species-specific responses, non-stocked plots were removed if a tree species was absent from both pre- and post-disturbance measurements of a plot. Of a total of 56 postfire plots sampled, *P. tremuloides*, *B. papyrifera*, *P. banksiana*, *P. mariana*, *P. glauca*, and *A. balsamea* were present in 41, 51, 34, 35, 34, and 55 plots, respectively, as a component species in the prefire, postfire, or both stand measurements. Of 47 post-clearcutting plots, *P. tremuloides*, *B. papyrifera*, *P.*

banksiana, *P. mariana*, *P. glauca*, and *A. balsamea* were present in 39, 35, 30, 44, 31, and 37 plots.

According to the Levene's and Kolmogorov-Smirnov's tests, heterogeneity of variances and normality were best achieved by transforming regeneration densities of *P. tremuloides*, *B. papyrifera* and *P. banksiana* by square root and regeneration densities of *P. mariana*, *P. glauca* and *A. balsamea* by $\log_{10}(y+1)$. The effects of disturbance and pre-disturbance species basal area on species specific regeneration density were tested using the univariate general linear model (SPSS Inc., 2006) (eq. 1).

$$Y_{ijk} = \mu + D_i + BA_j + D \times BA_{ij} + \varepsilon_{(ij)k} \qquad [1]$$

where Y_{ijk} is species-specific post-disturbance tree density (stems/ha); μ is the mean of species density; D_i is disturbance type (i =1, 2), BA_j is species-specific pre-disturbance basal area of the stand (m^2/ha); ε is error term.

To facilitate testing whether the relative abundance of a tree species changed after disturbance, species-specific compositional differences between the pre- and post-disturbed stands (CD) were calculated as the difference between post-disturbance relative density, i.e., species-specific regeneration density divided by total density of the stand, and pre-disturbance relative basal area (*sensu* Chen and others 2009). A positive CD indicates that relative abundance of a species after disturbance has increased, while a negative value reflects a decrease. Whether species-specific CD differs from zero was tested by Student's t-test separately for fire and clearcutting. To specify influence of disturbance type the species-specific CD was tested also by general linear model that

included disturbance type (fire or clearcutting), species-specific pre-disturbance relative abundance, and their interaction as predictors.

RESULTS

Post-disturbance regeneration was largely dominated by *P. tremuloides*, *B. papyrifera*, and *P. banksiana* in both postfire and post-clearcutting stands (Figure 3.1). Regeneration density was positively related to pre-disturbance basal area for *P. tremuloides*, *B. papyrifera*, *P. banksiana* and *P. mariana*, indicating a strong influence of propagule availability on post-disturbance regeneration (Table 3.1, Figure 3.2). However, no correlation was found for *P. glauca* and *A. balsamea.*

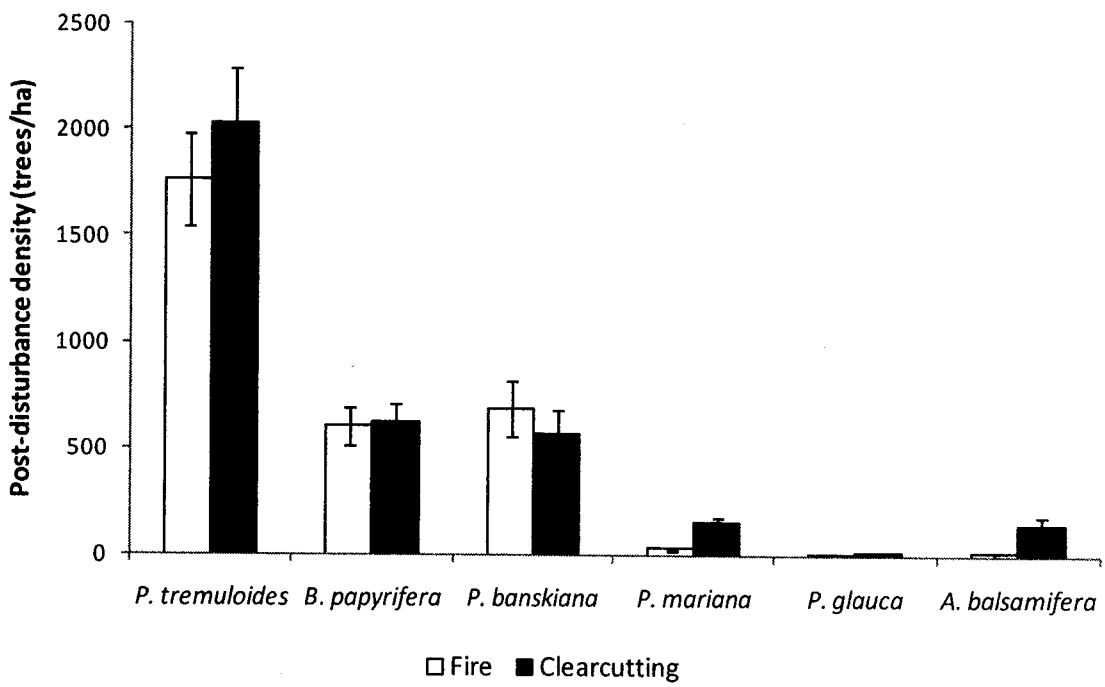

Figure 3. 1 Species-specific regeneration density (trees/ha) after fire and clearcutting (Mean ±1 SE).

Table 3. 1 Results of general linear model analyses. Post-disturbance density (trees/ha) is square root transformed for *P. tremuloides*, *B. papyrifera* and *P. banskiana*, and $\log_{10}$ (y+1) transformed for *P. mariana*, *P. glauca* and *A. balsamea*. Independent variables are disturbance type (D, fire *vs.* clearcutting) and species-specific pre-disturbance basal area (BA, m^2/ha).

Species	Source	Type III Sum of Squares	df	Mean Square	F	Sig.
P. tremuloides	D	0.4528	1	0.4528	0.0016	0.969
	BA	10394.2680	1	10394.2680	35.7802	<0.001
	D x BA	656.2405	1	656.2405	2.2590	0.137
B. papyrifera	D	819.1756	1	819.1756	7.1324	0.009
	BA	1390.4122	1	1390.4122	12.1061	0.001
	D x BA	20.1738	1	20.1738	0.1757	0.676
P. banksiana	D	3.8792	1	3.8792	0.0263	0.872
	BA	2394.7466	1	2394.7466	16.2292	<0.001
	D x BA	48.0658	1	48.0658	0.3257	0.570
P. mariana	D	5.2671	1	5.2671	8.1676	0.006
	BA	17.7819	1	17.7819	27.5742	<0.001
	D x BA	0.5384	1	0.5384	0.8350	0.364
P. glauca	D	1.0647	1	1.0647	2.5316	0.117
	BA	0.8993	1	0.8993	2.1384	0.149
	D x BA	0.6278	1	0.6278	1.4928	0.226
A. balsamea	D	16.1031	1	16.1031	26.5030	<0.001
	BA	0.0957	1	0.0957	0.1575	0.692
	D x BA	0.0176	1	0.0176	0.0289	0.865

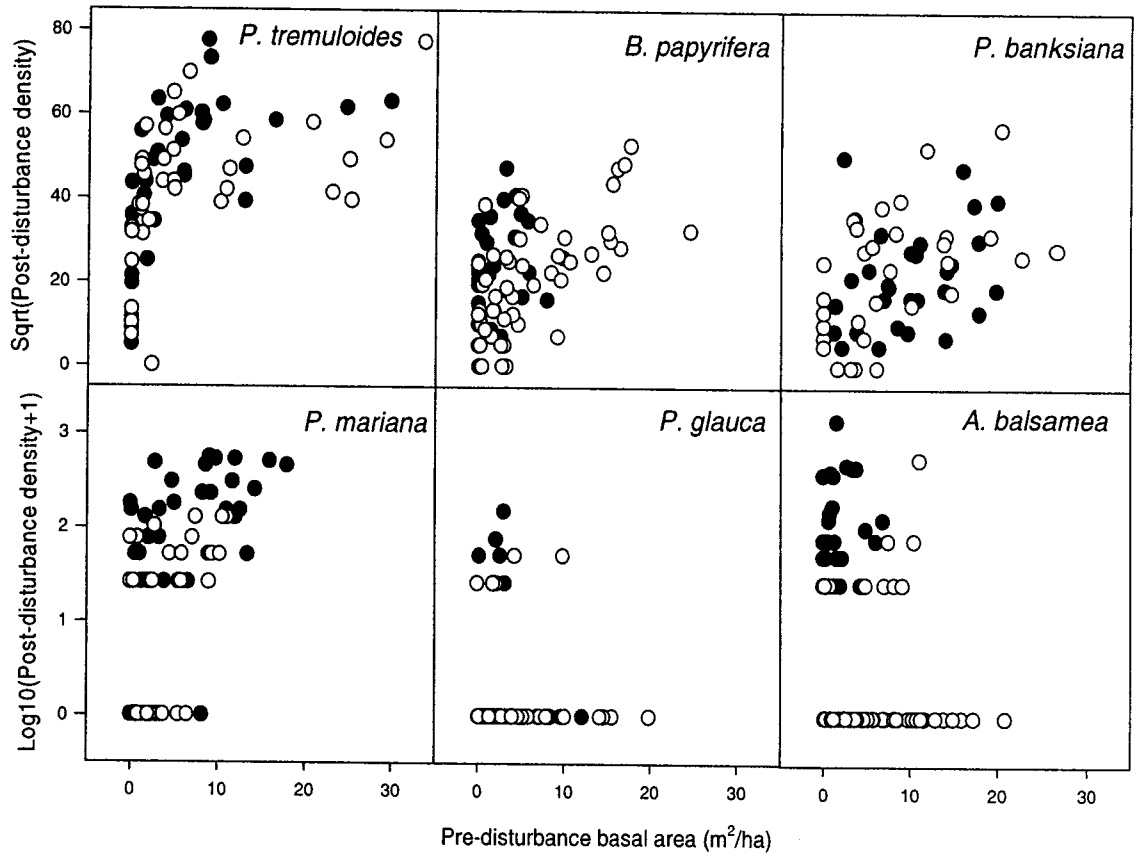

Figure 3. 2 The relationship between post-disturbance regeneration density (trees/ha) and pre-disturbance basal area (m^2/ha).White circles are for postfire and black circles for post-clearcutting.

Regeneration density did not differ significantly between the two disturbances for shade-intolerant species *P. tremuloides* and *P. banksiana* (Figure 3.2), but did for intermediate shade-tolerant and shade-tolerant species, except for *P. glauca*. For pre-disturbance stands that had a basal area of *B. papyrifera* $\leq$ 10 m^2/ha, post-disturbance regeneration density of *B. papyrifera* was higher in post-clearcutting sites than in postfire sites (Table 3.1, Figure 3.2). Regeneration densities of *P. mariana* and *A. balsamea* were significantly higher after clearcutting than after fire (Figure 3.2). With

few exceptions, fire resulted in no regeneration of *A. balsamea* (Figure 3.2). *P. glauca* regeneration was mostly absent from both disturbances (Figure 3.2).

Compositional difference between post- and pre-disturbance stands (CD) was significantly positive, approximately 35% for *P. tremuloides* after both fire and clearcutting, and 22% and 11% for *B. papyrifera* after fire and clearcutting, respectively (Table 3.2, Figure 3.3). For *P. banksiana*, CD did not differ from zero after both disturbances. For both *P. mariana* and *P. glauca,* CD was significantly negative after both disturbances, whereas for *A. balsamea*, CD was significantly negative after fire, but did not differ from zero after clearcutting (Figure 3.3).

Table 3. 2 Student's t-test of species-specific compositional difference after fire and clearcutting. Difference from zero is tested.

Species	Disturbance	t	df	Sig. (2-	Mean
P. tremuloides	Fire	10.097	40	<0.001	36.061
	Clearcutting	9.606	38	<0.001	34.270
B. papyrifera	Fire	5.579	50	<0.001	22.149
	Clearcutting	2.632	34	0.013	10.853
P. banskiana	Fire	-1.825	33	0.077	-7.342
	Clearcutting	-2.008	29	0.054	-11.357
P. mariana	Fire	-5.681	34	<0.001	-16.164
	Clearcutting	-5.720	42	<0.001	-18.946
P. glauca	Fire	-3.160	33	0.003	-13.581
	Clearcutting	-5.041	30	<0.001	-13.893
A. balsamea	Fire	-10.216	54	<0.001	-23.994
	Clearcutting	-1.845	36	0.073	-4.505

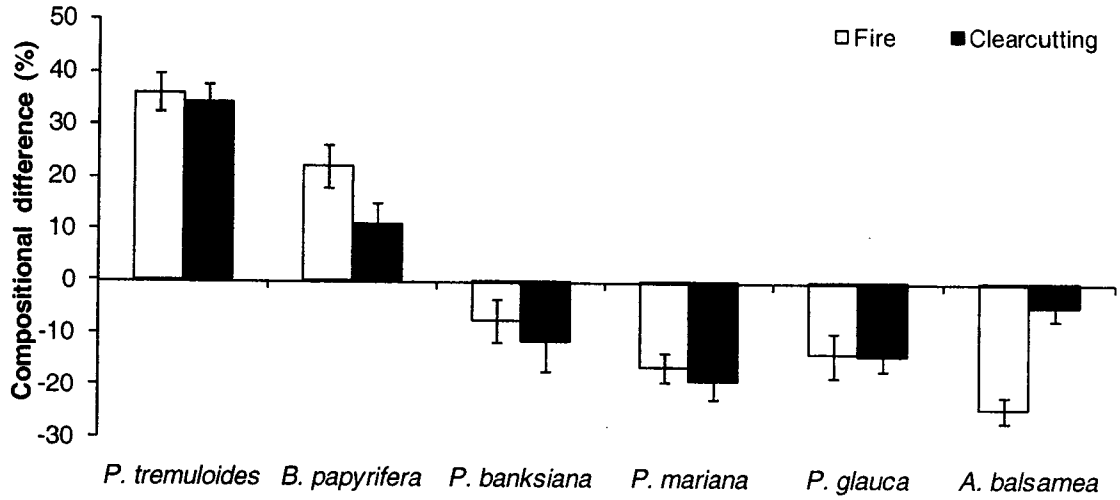

Figure 3. 3 Compositional difference (%) of post- and pre-disturbance stands of six tree species after fire and clearcutting (Mean ±1 SE).

Our examination of CD in relation to species-specific pre-disturbance basal area percentages showed that CD decreased with increasing pre-disturbance basal area percentage for *B. papyrifera* and all coniferous species after both disturbances (Figure 3.4, Table 3.3). For *P. tremuloides*, CD increased and peaked at approximately 20% of its pre-disturbance basal area percentage and then decreased (Figure 3.4), indicating that *P. tremuloides* can regenerate with a high sapling density after disturbance with the presence of few parent trees before disturbance. With incorporation of pre-disturbance basal area percentage as a predictor, CD of *A. balsamea* was only species that showed smaller CD values after fire than clearcutting (Figure 3.4, Table 3.3).

Table 3. 3 Results of general linear model analyses of species-specific compositional difference between the post- and pre-disturbance stand (CD, %) with disturbance type (D, fire *vs.* clearcutting) and species-specific pre-disturbance relative abundance (BA, %), and their interaction as predictors.

Species	Source	Type III Sum	df	Mean	F	Sig.
P. tremuloides	D	453.48	1	453.48	0.880	0.3510
	BA	89.00	1	89.00	0.173	0.6788
	D x BA	532.71	1	532.71	1.034	0.3124
B. papyrifera	D	356.89	1	356.89	0.551	0.4599
	BA	489.97	1	489.97	0.757	0.3869
	D x BA	6,280.53	1	6,280.53	9.701	0.0025
P. banksiana	D	20.41	1	20.41	0.033	0.8555
	BA	9,172.71	1	9,172.71	15.23	0.0003
	D x BA	93.43	1	93.43	0.153	0.6971
P. mariana	D	64.10	1	64.10	1.068	0.3047
	BA	22,545.99	1	22,545.99	375.65	<0.0001
	D x BA	174.34	1	174.34	2.906	0.0925
P. glauca	D	61.28	1	61.28	0.365	0.5482
	BA	16,699.39	1	16,699.39	99.62	<0.0001
	D x BA	2.17	1	2.17	0.013	0.9099
A. balsamea	D	261.82	1	261.82	8.579	0.0043
	BA	16,084.21	1	16,084.21	527.57	<0.0001
	D x BA	0.80	1	0.80	0.026	0.8721

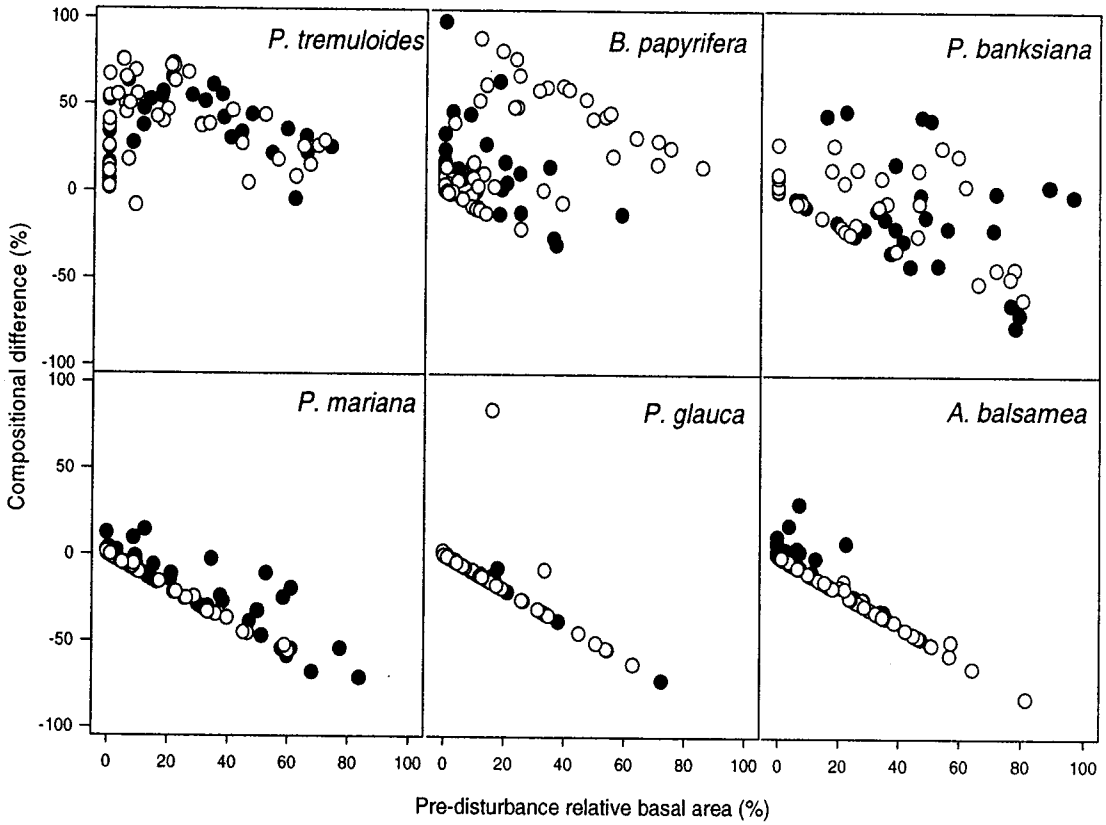

Figure 3. 4 Species-specific compositional difference (%) as a function of species pre-disturbance relative basal area. White circles are for postfire and black circles for post-clearcutting.

DISCUSSION

Stand basal area of parent tree species is a good predictor of species-specific regeneration density as it is directly related to propagule availability (Lavoie and Sirois, 1998; Greene and others, 2004). In this study, significant relationships between regeneration density and pre-disturbance basal area were found for all studied species after both fire and clearcutting. Differences in regeneration success between burned and

clearcut stands can be explained by effects of species specific propagule availability and substrate as discussed separately for each species below.

P. tremuloides responded with similar high regeneration densities to fire and clearcutting. The increase of *P. tremuloides* after disturbance can be attributed to the nature of each disturbance and capacity of the species to vigorously regenerate vegetatively. Both disturbances kill parent trees, eliminating apical dominance and increasing the ratio of cytokinins (produced by roots) to auxins (produced by shoots), resulting in increased production of root suckers (Farmer, 1962; Eliasson, 1971; Steneker, 1974). Fire and clearcutting also tend to moderately wound roots, promoting suckering (Fraser and others, 2004b). Smaller regeneration densities after fire are more likely after very severe fires as they usually destroy roots of *P. tremuloides* (Wang, 2003).

High densities of *P. tremuloides* regeneration, up to 6,000 trees per hectare compared to maximum densities of two other shade-intolerant species *P. banksiana* (3,250 trees/ha) and *B. papyrifera* (2,775 trees/ha), and increased proportions in post-disturbance stands are reported by a number of studies (e.g.Bergeron and Charron, 1994; Carleton and MacLellan, 1994; Lavertu and others, 1994; Mallik and others, 1997). Prolific suckering and rapid growth of stems make *P. tremuloides* extremely competitive after fire and clearcutting since carbohydrate reserves in the roots of parent trees provide suckers with nutrients during the most competitive years following disturbance, facilitating rapid height growth and occupation of available space compared to seedlings (Frey and others, 2003). In addition, contrary to *B. papyrifera* which is capable of

developing from basal buds, the extensive clonal root system of *P. tremuloides* (Kemperman and Barnes, 1976) with numerous shallow widely spreading roots (Strong and Laroi, 1983) allows it to extend the zone of colonization.

Fire and clearcutting had different effects on *B. papyrifera* densities. In burns, the relationship between pre-fire basal area and regeneration density was strongly positive, while in clearcuts, densities varied from zero to 2,225 trees per hectare and had a weaker relationship with pre-disturbance basal area. Similarly, the proportion of birch increased following fire by 22%, while after clearcutting CD was only 11%. Regeneration from buds is relatively vigorous after both fire and clearcutting (sprouting from 30-90% of stumps and snags) (Perala and Alm, 1990), but is restricted to the location of stumps or snags of parent trees. Since *B. papyrifera* trees are typically left uncut in the study area during clearcutting (Brassard and Chen, 2008), the lower abundance of *B. papyrifera* after clearcutting is likely attributed to the inability of dying trees to sprout.

The lack of vegetative colonization of *B. papyrifera* can be compensated by seed dispersal and seedling recruitment. The best substrates for *B. papyrifera* germination, survival and subsequent growth are lightly shaded (protects soil from drying) mixes of mineral soil and organic material. Mineral soil provides better moisture retention for germination and organic substances supply seedlings with nutrients (Marquis and others, 1964; Perala and Alm, 1990). These conditions are abundant in fire areas, where snags and downed logs provide some shade and fire has destroyed competing vegetation and litter, as opposed to clearcuts where the tree layer is removed and soil damage is random

(Nguyen-Xuan and others, 2000; McRae and others, 2001). In large disturbance areas, however, seed sources may be limited despite *B. papyrifera* having very light seeds compared to most other boreal tree species (Hewitt, 1998). Perala and Alm (1990) found the majority of *B. papyrifera* seeds fall within a 50 m radius of the parent tree and only a small fraction of seeds are distributed beyond 100 meters. As we established all our plots at least 50 m away from the forest edge or survived trees, regeneration of *B. papyrifera* appears to be mostly from sprouting.

P. banksiana and *P. mariana* are two boreal tree species that have serotinous cones, an adaptation to fire which promotes the distribution of seeds to favorable seedbeds when high temperatures cause cone opening and seed release (Lamont and others, 1991). We therefore expected that fire would promote regeneration of these species while clearcutting would result in a decrease or local extirpation. However, *P. banksiana* responded to clearcutting with similar densities to fire. Post-clearcutting regeneration of *P. banksiana* is highly dependent on the level of canopy removal and the mechanical disturbance of the forest floor that exposes mineral soil (Eyre, 1938). Clearcutting with duff removal treatments can result in approximately 25,000 seedlings/ha of *P. banksiana* (Eyre, 1938). It appears that mechanical clearcutting in our study had created sufficient mineral exposure to provide sufficient favorable seedbeds and increased soil surface temperatures, resulting in a similar effect on cone opening as fire.

P. mariana had lower densities following both fire and clearcutting. Fire, however, resulted in low densities (maximum 125 trees/ha), while clearcutting provided

somewhat higher regeneration densities (maximum 550 trees/ha). This may indicate that despite the presence of an aerial seed bank, black spruce is not always capable of regeneration shortly after fire as shown by St-Pierre et al (1992). The difference in our findings and those from St-Pierre (1992) may be attributed to the differences in forest ecosystem type (boreal mixedwoods *versus* black spruce and jack pine dominated conifer type) or climate region, possibly explaining why black spruce is more abundant in east than west on uplands.

In our study, seedling limitation cannot be attributed to a destroyed seed bank (Arseneault, 2001) because the fire in our study occurred early in the season, which is typically less intense than fires occurring in late summer. As well, pre-disturbance stands were mature enough to have sufficiently large seed banks. The limited regeneration of *P. mariana* is most likely due to unsuitable seedbed conditions before and after fire (Foster, 1985; Lavoie and Sirois, 1998). Charron and Green (2002) demonstrated with sowing experiments that mineral soil, thin moss layer, and humus are more favourable seed beds than burnt organic fermenation (OF) and litter seed beds. Futhermore, they also reported that following spring fires (like the fire in our study) more than 80% of the area was covered with burnt Of layer, explaining low densities of *P. mariana* seedlings. Post-fire seedling suppression by more aggressive species (i.e., *Populus* spp.) may be another negative effect on *P. mariana* seedling density (Johnstone and others, 2004). In addition, there may not have been sufficient time for *P. mariana* to reach regeneration potential since its post-disturbance regeneration density of *P. mariana* has been found to be strongly related to time since disturbance in a post-

logging study (Chen and Wang, 2006) and a large-scale postfire regeneration study (Chen and others, 2009). *P. mariana* has been reported to act as a late-successional species on upland sites, increasing its proportion over 100 years (Harper and others, 2002). In clearcuts, higher densities of *P. mariana* are generally due to the survival of advance regeneration (Haeussler and Bergeron, 2004; Simon N. and Schwab, 2005).

A. balsamea and *P. glauca* have limited capacity to reproduce vegetatively or disperse seeds over long-distances, and they do not have aerial seed banks. Therefore, the absence of these species in post-fire stands is largely attributed to seeding limitation. In clearcuts, *A. balsamea* was found to be relatively abundant, while densities of *P. glauca* were close to zero. The difference in regeneration density after clearcutting is attributable to their abundance in the understory of pre-disturbance stands, where *A. balsamea* is common in the study area (Ilisson and Chen, personal observations). Survival of advance regeneration can depend on harvesting methods, equipment, and season according to several studies (Harvey and Bergeron, 1989; Harvey and Brais, 2002; Simon N. and Schwab, 2005). With careful harvesting, densities as high as 30,000 trees per hectare of *A. balsamea* have been reported (Harvey and Brais, 2002).

CONCLUSIONS

In the central boreal mixedwood forest, development of post-disturbance composition depends on pre-disturbance species composition and disturbance type. *P. tremuloides* regenerates with very high densities following fire and clearcutting. If, in the pre-disturbance stand, *P. tremuloides* is represented by even a few individuals, it is likely that this species will dominate the post-disturbance stand because suckering

allows it to regenerate aggressively with high sapling numbers and makes it a very strong competitor for space and resources after disturbance. *B. papyrifera* had somewhat higher densities after fire than after clearcutting, perhaps attributed to the inability of slowly dying trees to sprout in clearcuts and better mineral exposure after fire that promotes its regeneration by seeds. *P. banksiana* responded similarly to fire and clearcutting despite its serotinous cones. Cones of *P. banksiana* seem to be capable of seed release from high ground temperatures that resulted from the forest floor disturbances created by mechanical harvesting. Both *B. papyrifera* and *P. banksiana* can produce high regeneration densities relative to their pre-disturbance representation in the stand. However, their proportions and subsequent survival are likely related to the presence and abundance of the more competitive *P. tremuloides*. Fire causes local extirpation or very low densities of *P. mariana*, *P. glauca*, and *A. balsamea*, while clearcutting enables *P. mariana* and *A. balsamea* – shade-tolerant species that are capable of establishing in the understory – to establish in the post-disturbance stand. It is possible that survival of these species may facilitate the transition of softwood dominance sooner in clearcuts than in burns – in addition to their presence; older advance regeneration trees may represent a valuable seed source for later recruitment. However, regeneration densities of these species were low, showing that the proportion of these conifers in post-cut stand compositions is fairly low at the early stages of stand development. The natural regeneration recruitment after fire appears to be emulated by clearcutting for *P. tremuloides*, *P. banksiana*, *P. mariana*, and *P. glauca*, but the increase of *B. papyrifera* after clearcutting is less pronounced than after fire, while the reduction of *Abies balsamea* after clearcutting is less severe than after fire.

CHAPTER 4. TREE HEIGHT GROWTH AND LIVE TREE STRUCTURAL DIVERSITY OF BOREAL MIXEDWOODS AFTER FIRE AND CLEARCUTTING

INTRODUCTION

The Canadian boreal mixedwood forest forms complex landscapes with stands composed of one to several tree species in varying ratios. Historically, fire has been the main stand-replacing disturbance shaping the landscape. Heterogeneous fire cycles (Weir and others, 2000; Bridge, 2001), combined with varying fire severity from mild ground fires to severe crown fires, have created diverse species compositions. Clearcutting, which has become an important anthropogenic disturbance in the boreal mixedwood forest during the last century, may have a strong influence on post-cut stand composition, productivity, and structure. Although clearcutting has been proposed by forest managers as a management option to mimic fire, its effects on boreal mixedwood forest development are poorly understood.

Both fire and clearcutting shift species composition towards higher broadleaf proportions (Archambault and others, 1998; Greene and others, 1999; Lepage and others, 2000; Greene and others, 2004; Chen and others, 2009; Ilisson and Chen, 2009a; Ilisson and Chen, 2009b). Compared with fire, clearcutting tends to retain a small proportion of late-successional conifers, mainly black spruce (*Picea mariana* (Mill.) B.S.P.) and balsam fir (*Abies balsamea* (L.) Mill.), in the post-disturbance stand (Nguyen-Xuan and others, 2000; Harvey and others, 2002). However, only a few studies

have examined the influence of these disturbances on tree height growth and live tree structure. Tree height growth rate is of interest to forest managers as it determines the economic value of the forest, while stand structure is related to habitat suitability, aesthetical values, fire hazard, and vulnerability to insects and/or fungi through its effects on soil characteristics, temperature, and light environment (Varga and others, 2005; Brassard and Chen, 2006; Brassard and others, 2008).

Because both fire and clearcutting have some distinctive effects on stand nutrient dynamics and soil properties, tree growth and structural development may differ significantly following the two disturbances. Even though the losses of nitrogen are comparable after both disturbances, clearcutting, unlike fire, removes large amounts of phosphorus, potassium, calcium, and magnesium contained in the tree biomass (McRae and others, 2001). Fire results in increased pH and nutrient retention because of charcoal addition (Zackrisson and others, 1996), while clearcutting negatively affects vegetative reproduction due to soil compaction (Fraser and others, 2004a). In addition to the effect of disturbance type, faster nutrient cycling in stands with a broadleaf component (Reich and others, 2001) may affect tree height growth.

Furthermore, as tree height growth may also be driven by the influence of inter- and intra-specific competition, competition for light and other resources in stand types with high regeneration density may result in reduced height growth compared with stand types with low regeneration density (Huang and Titus, 1999). Since stand structure of live trees can be described by height or diameter variation (vertical and horizontal structural diversity, respectively), stand structure is expected to differ with disturbance and stand type. In particular, mixed-species stand types are likely more structurally

diverse than single-species stands because of differences in growth rates among tree species (Johnstone and others, 2004; Varga and others, 2005; Brassard and Chen, 2006).

The purpose of this study was to examine growth and structure of live trees in post-fire and post-clearcutting stands. We studied (1) the influence of disturbance and post-disturbance stand type on the annual tree height growth rate for six boreal tree species – trembling aspen (*Populus tremuloides* Michx.), paper birch (*Betula papyrifera* Marsh.), jack pine (*Pinus banksiana* Lamb.), black spruce, white spruce (*P. glauca* (Moench) Voss), and balsam fir, and (2) stand vertical and horizontal structure of live trees that resulted from fire and clearcutting.

We hypothesized that: (1) the annual height of all studied species (except advance regeneration trees) is higher after fire than after clearcutting because of more favorable soil nutrient conditions and lack of competitive residual understory vegetation in fire areas; (2) the annual height growth rate is lower in stands of very low density since there is no need to invest in height growth to compete for light resources or stands of very high densities because the limited resources inhibit height growth; (3) stand structure of live trees is more diverse in clearcuts than in burnt areas because survival of advance regeneration may increase vertical structural diversity, and also the presence of compacted soil patches due to forest machinery movement that may increase horizontal structural diversity.

METHODS

STUDY AREA

We sampled both post-fire and post-clearcutting sites in the boreal mixedwood forest of northwestern Ontario (Spruce River Forest and the Black Sturgeon Forest. The study area is in the boreal forest north of Lake Superior and west of Lake Nipigon in the Upper English River (B.11) Forest Regions (Rowe 1972), approximately 150 km north of Thunder Bay, Ontario (48° 22' N, 89° 19' W, 199 m elevation). The study area has a moderately dry, cool climate with short summers. The average annual precipitation for Thunder Bay (1971-2000) is 712 mm and the average annual temperature is 2.5 °C (Environment Canada, 2007). The area belongs to the moist mid-boreal ecoclimatic region (Ecoregions Working Group (EWG), 1989). Topographic features were shaped by the retreat of the Laurentide Ice Sheet approximately ten millennia ago, resulting in rolling topography.

The region is part of the boreal mixedwood forest, with upland forests consisting primarily of mixtures of *P. tremuloides*, *B. papyrifera*, *P. banksiana*, *P. mariana*, *P. glauca*, and *A. balsamea* with a small contribution from red pine (*Pinus resinosa* Ait), white pine (*Pinus strobus* L.), tamarack (*Larix laricina* (Du Roi) K. Koch), and Eastern white cedar (*Thuja occidentalis* L.) on some sites (Rowe 1972). Fire is the most common natural stand-replacing disturbance in the study area. The last spruce budworm (*Choristoneura fumiferana* Clem.) epidemic peaked in 1986 and collapsed approximately 10 years later (Paul Poschmann, personal communication), causing significant mortality of host-specific trees (i.e., *A. balsamea* and *Picea* spp.). The soil

type is sandy loam eluviated dystric brunisoil (Soil Classification Working Group, 1998). Sandy loam soils are generally favorable for tree establishment and growth (Brady and Weil, 2004). These soils, with moderate water holding and nutrient storage capacity, warm up faster in spring, promoting bud initiation and seed germination.

FIELD MEASUREMENTS

Field data collection took place in the summer 2007. To facilitate sampling, a wide range of pre-disturbance stand composition areas were selected using forest inventory maps. Pre-disturbance stand ages ranged from 80 to 150 years. Since most natural regeneration processes of boreal tree species are completed within five years after fire and clearcutting (Lavoie and Sirois, 1998; Gutsell and Johnson, 2002; Johnstone and others, 2004), we selected both post-fire and post-clearcutting stands approximately 5 to 15 years after the stand replacing disturbance, similar to Chen and others (2009).

It is difficult to have a well-balanced design to study the effects of natural disturbances (Turner and others, 1997; Parker and Wiens, 2005). In the study area, there was one large fire that occurred during the decade of interest (1992-2002), which took place on April 30th, 1998, and burnt approximately 26,400 ha of various stand types and site conditions. Fire qualifies as a light severity fire – overstory trees were killed, litter was burned, but the duff layer was only partially consumed (*sensu* Wang (2002)). Post-clearcutting stand ages ranged from 6 to 12 years from operations occurring between 1995 and 2001. All sites were harvested in the whole tree harvesting method – trees

were cut and then cleaned from branches on the signed lots or by the roadside. Clearcutting in all study plots took place in winter or early spring. Therefore, the apical dominance of vegetatively reproducing species was eliminated before development of spring foliation and as such levels of carbohydrates should be similar in fire and clearcutting areas. All selected fire sites were left to regenerate naturally without salvage logging or other treatments. To minimize the possibility of seeds from undisturbed areas, the plots were established a minimum of 250 meters from unburned or uncut forest edges. To minimize the influence of silviculture on natural regeneration, we did not select any site that had received site preparation, seeding, or vegetation management. However, because of limited availability of untreated *P. banksiana* dominated stands, which typically receive seeding or planting treatment in the study area, we included several sites that did not receive any other silvicultural treatments except spot planting, but planted trees were excluded from analyses.

In total, we sampled 56 post-fire stands and 47 post-clearcut stands. Every effort was made to intersperse stands to avoid sampling stands in close proximity to one another in order to minimize the impact of spatial structure (Legendre and Legendre, 1998). To limit site variability, all sites were located on flat, mid slope positions, with no slope exceeding 5%, on well-drained glacial moraines greater than 50 cm in thickness. This is the prevailing site type in the region. In the field, site condition was determined by topographic characteristics in each sampled stand.

On each selected site, pre-disturbance stand structure and composition were determined by a 20 x 20 m plot. Within the plot, only live trees at the time of the fire or

logging were measured. Dead trees that had been killed by fire or logging still had solid structure after 5 to 15 years. Tree species were identified based on bark recognition, mode of regeneration, and architecture, as described in Chen and others (2009). We measured breast-height diameters (1.3 m high) in the post-fire stands and root-collar diameters on stumps in clearcut stands. To calculate breast height diameter for trees in clearcuts, models of root-collar to breast-height diameter relationships for each of the six tree species were created by collecting data from surrounding intact stands. For each species, one hundred trees of variable sizes were randomly selected for diameter measurements.

Post-disturbance regeneration was assessed in three randomly located 5 x 5 m subplots in the 20 x 20 m plot that was used to determine the pre-disturbance stand condition. All regenerating tree species were identified, tree heights were measured and trees were counted in the subplots.

ANALYSIS

Post-disturbance stand types were determined based on species-specific post-disturbance regeneration densities using a hierarchical clustering method. Ward group linkage method with Euclidean distance measure, which is considered a reliable and effective method of clustering (McCune and Grace, 2002), was used. The resulting dendrogram was scaled by Wishart's objective function converted to a percentage of information remaining. The dendrogram of regeneration density of six species was trimmed at seven post-disturbance stand types. The dendrogram accounted for 75% of

the variation of species-specific regeneration densities. The post-disturbance stand types and regeneration densities are given in Table 1 and species-specific compositions in Figure 4.1. The hierarchical clustering analysis was performed using the statistical package PC-ORD version 5.14 (McCune and Mefford, 2006). Total stand density (trees/ha) was significantly different among stand types (Table 4.2). The order from highest density to lowest is: PO, PJ, PoBw, PoPj, BW, PjLow, BwLow.

All post-disturbance stand types were broadleaf or jack pine dominated. However, the pre-disturbance composition of the same study plots was composed of different proportions of trembling aspen, paper birch, jack pine, black spruce, white spruce, and balsam fir. Analyzing species-specific responses to fire and clearcutting in the same study area, Ilisson and Chen (2009) found a strong positive relationship between pre- and post-disturbance proportions for trembling aspen, paper birch, and jack pine, and the proportions of these species increased significantly after disturbance, resulting in a shift of mid-or late-successional conifer-dominated stand types to early-successional stand types. To be able to interpret some of the results, pre-disturbance composition must be considered.

Table 4. 1 Post-disturbance stand type groups and their characteristics according to hierarchical clustering. Associated species represents those occurred in most stands within the stand type. Stand types are described in text. Species codes are: Po – trembling aspen, Bw – paper birch, Pj – jack pine, and Sb – black spruce.

Stand type	Regeneration density of all species (trees/ha, mean±1 SE)	Regeneration density range of dominant species (trees/ha, min-max)	Associated species
PO	4555±220	Po: 2850-6000	Bw, Pj
PoBw	3139±233	Po: 1075-2225; Bw: 950-1650	
PoPj	2723±133	Po: 1000-2900; Pj: 25-1600	Bw, Sb
PJ	3588±282	Pj: 2250-3250	Bw, Po
PjLow	1111±121	Pj: 350-1600	Sb
Bw	2384±134	Bw: 1275-2775	
BwLow	731±100	Bw: 50-1200	

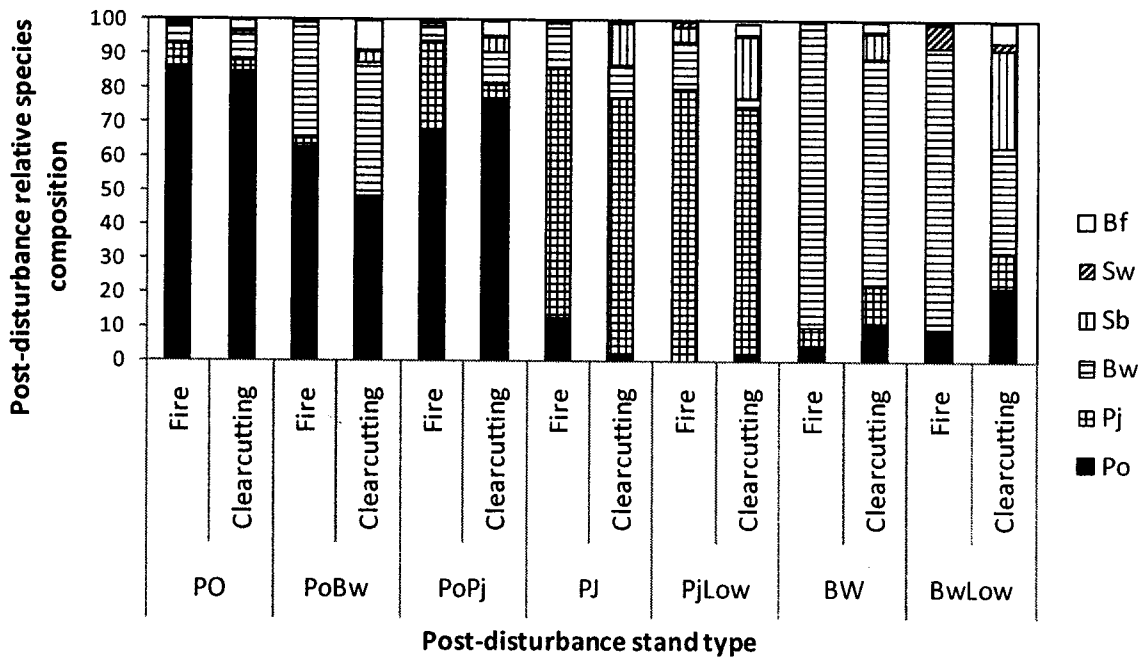

Figure 4. 1 Post -disturbance relative species proportions based on relative tree density in seven stand types.

Table 4. 2 Effects of time since disturbance (TSD,covariant), disturbance type (D), and post-disturbance stand type (S) on stand density (trees/ha).

Source	Type III sum of squares	df	Mean square	F	P
TSD	1178851	1	1178851	2.51061	0.1167
D	172907	1	172906.6	0.368241	0.5455
S	142923298	6	23820550	50.73086	<.0001
D x S	3190396	6	531732.6	1.132436	0.3503

Annual height growth was analyzed separately for each of the six species. Mean annual height growth rate was calculated by dividing regeneration tree height by time since disturbance. Mean annual height of stems was then averaged for each species in each study plot. Annual height of balsam fir was square root transformed to achieve homogeneity of variances and normality.

Post-disturbance live tree structure was analyzed using the following structural indices: regeneration density, Shannon Index (H') for species diversity, Gini coefficient (GC) for height variation and Cox index of clumping (CI) for spatial variation. Formulas and calculations of these indices are given in Table 4.3. Density and H' were square root transformed and CI and GC indices were $\log_{10}$ transformed to achieve normality and homogeneity of variances.

Table 4. 3 Indices for species and structural diversity. S – number of species in the plot; p_i – proportion of *i*th species in the stand; n_i - the number of individuals in the '*i*th' species; N – total number of trees; $_j$ – the rank of a tree in ascending order from 1,…,n; ba_j – basal area of the *j*th tree; s_x^2 - variance of regeneration tree density between three sub-plots within a sample plot; $\bar{x}$ - mean number of stems on sub-plots within the study plot.

Index	Formula	Studied diversity component	Reference
Shannon index	$H' = -\sum_{i=1}^{S} p_i \ln(p_i)$	Tree species diversity	(Shannon, 1948; Lexerod and Eid, 2006)
Gini coefficient	$GC = \frac{\sum_{j=1}^{N}(2j-N-1)ba_j}{\sum_{j=1}^{N} ba_j(N-1)}$	Diameter and height diversity	(Lexerod and Eid, 2006)
Cox Index of clumping	$CI = \frac{s_x^2}{\bar{x}}$	Variation in species spacing	(Neumann and Starlinger, 2001; Montes *and others*, 2005)

All variables described above were analyzed using a univariate general linear model (GLM) with disturbance type, post-disturbance stand type, and their interaction as independent variables. Time since disturbance was included as a covariant to account for the effect of stand ages. Hochberg's GT2 method post hoc test for unequal sample sizes was used to determine differences among means (Day and Quinn, 1989). Analyses were conducted in SPSS 16.0 for Windows (SPSS Inc., 2006).

RESULTS

The two broadleaf species had higher annual tree height growth rates compared with conifers. Mean annual height growth for both trembling aspen and paper birch was 0.26 m. Mean annual height growth for pine, balsam fir, black spruce, and white spruce was 0.17, 0.11, 0.08, and 0.11 m, respectively.

The effect of disturbance type on annual height growth differed with stand type for trembling aspen, jack pine, and white birch, while time since disturbance was not significant for height growth of any species except birch (Table 4.4, Figure 4.2). Aspen had a higher growth rate after clearcutting than fire in aspen dominated stand types (PO, PoBw and PoPj) and on BwLow sites, but lower on PJ sites (Table 4.4; Figure 4.2). Among stand types, aspen had a higher growth rate in aspen dominated stand types. Annual height growth of jack pine was higher in pine dominated or co-dominated stand types (PJ, PjLow and PoPj). Compared with fire, clearcutting reduced pine height growth in PJ and PjLow stand types, but increased height growth in PO and PoPj stand types (Table 4.4; Figure 4.2). Annual height growth of birch was significantly higher in broadleaf dominated stands than pine dominated stands. Clearcutting resulted in a significantly lower height growth rate of birch in all stand types except PoPj (Table 4.4; Figure 4.2).

Table 4. 4 Effects of time since disturbance (TSD), disturbance type (D) and post-disturbance stand type (S) on annual height growth. Annual height growth of balsam fir was square root transformed.

Analysis	Species	Source	Type III sum of squares	df	Mean square	F	P
1	Po	TSD	0.020	1	0.020	3.94	0.0514
		D	0.003	1	0.003	0.67	0.4153
		S	0.147	6	0.024	4.85	0.0004
		D ×S	0.111	5	0.022	4.38	0.0017
2	Pj	TSD	0.001	1	0.001	0.28	0.5983
		D	0.001	1	0.001	0.35	0.5593
		S	0.052	6	0.009	2.16	0.0635
		D ×S	0.049	5	0.010	2.46	0.0466
3	Bw	TSD	0.055	1	0.055	5.71	0.0199
		D	0.063	1	0.063	6.62	0.0124
		S	0.101	6	0.017	1.77	0.1198
		D ×S	0.209	6	0.035	3.64	0.0036
4	Sb	TSD	0.001	1	0.001	1.02	0.3187
		D	0.004	1	0.004	3.35	0.0749
		S	0.018	6	0.003	2.26	0.0577
		D ×S	0.007	3	0.002	1.84	0.1565
5	sqrt(Bf)	TSD	0.023	1	0.023	2.63	0.1167
		D	0.060	1	0.060	6.93	0.0141
		S	0.043	6	0.007	0.82	0.5632
		D ×S	0.029	3	0.010	1.11	0.3614

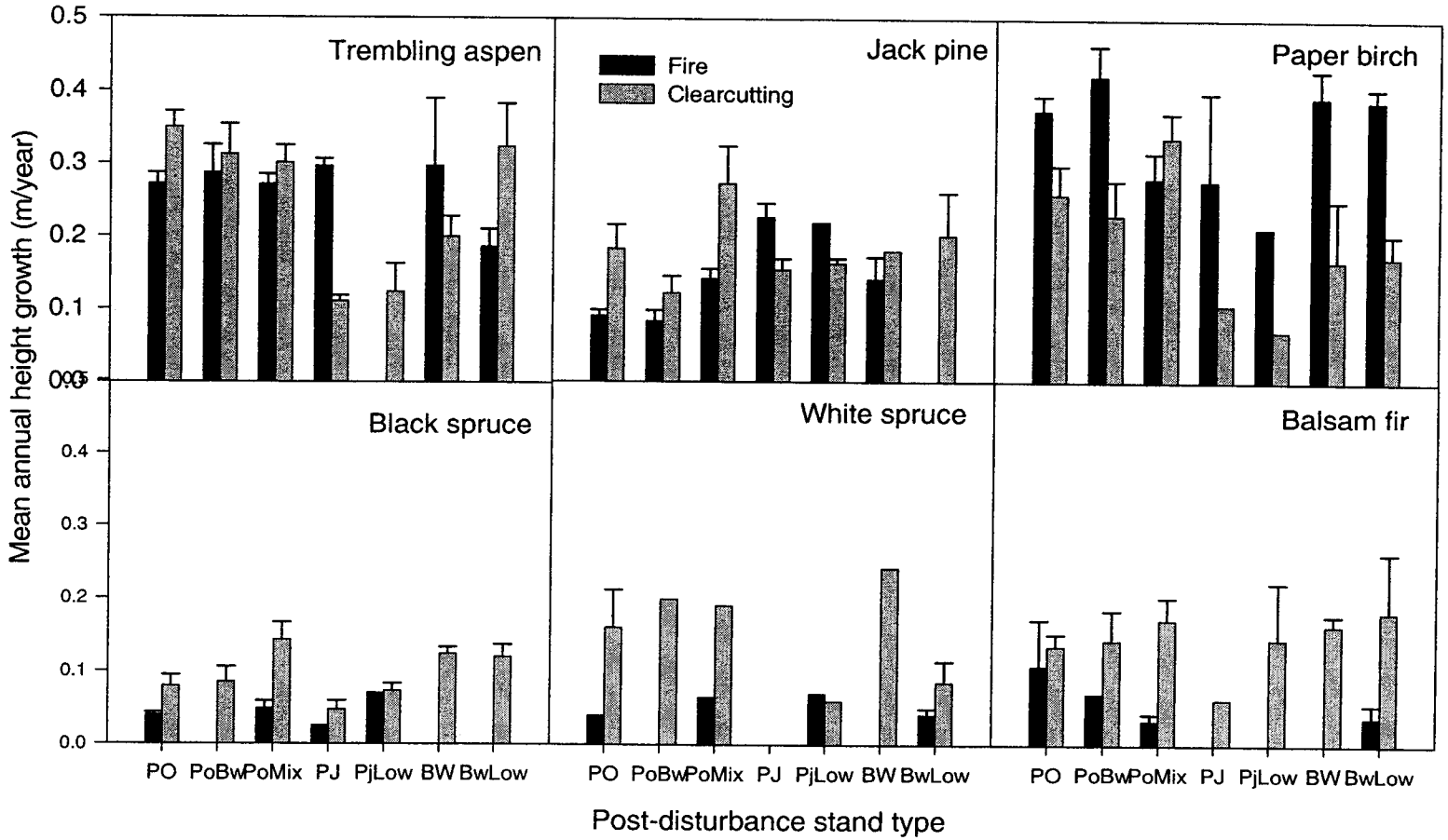

Figure 4. 2 Mean annual height of trembling aspen, jack pine, paper birch, black spruce, white spruce and balsam fir in post-disturbance stand types. Error bars are ±1 SE.

Mean annual height growth of mid- and late-successional conifers was generally higher after clearcutting than fire (Table 4.4; Figure 4.2) because of survival of advance regeneration. Height growth of balsam fir was consistently higher after clearcutting across all stand types. The effect of disturbance type and stand type was marginally significant on annual height growth of black spruce. Sample size was too small to allow an analysis of height growth response of white spruce to fire and clearcutting, since both disturbances largely eliminated this species from the stands.

Species diversity was higher after clearcutting than fire (Table 4.5; Figure 4.3). Among stand types, species diversity decreased in the following order: PoBw, PJ, PoPj, PjLow, BW, PO and BwLow. Neither Gini coefficient nor Cox Index of Clumping differed significantly with stand type or disturbance type.

Table 4. 5 Effects of disturbance type (D) and post-disturbance stand type (S) on diversity indices.

Analysis	Index	Source	Type III sum of	df	Mean	F	P
1	Sqrt(H')	D	0.34	1	0.34	4.39	0.0390
		S	1.21	6	0.20	2.59	0.0231
		D ×S	0.87	6	0.15	1.87	0.0955
2	Log_{10}(Gini	D	0.01	1	0.01	0.84	0.3628
	coefficent)	S	0.08	6	0.01	1.13	0.3510
		D ×S	0.14	6	0.02	1.94	0.0826
3	Log_{10}(Cox Index	D	0.54	1	0.54	2.05	0.1562
	of Clumping)	S	2.29	6	0.38	1.45	0.2034
		D ×S	2.62	6	0.44	1.66	0.1395

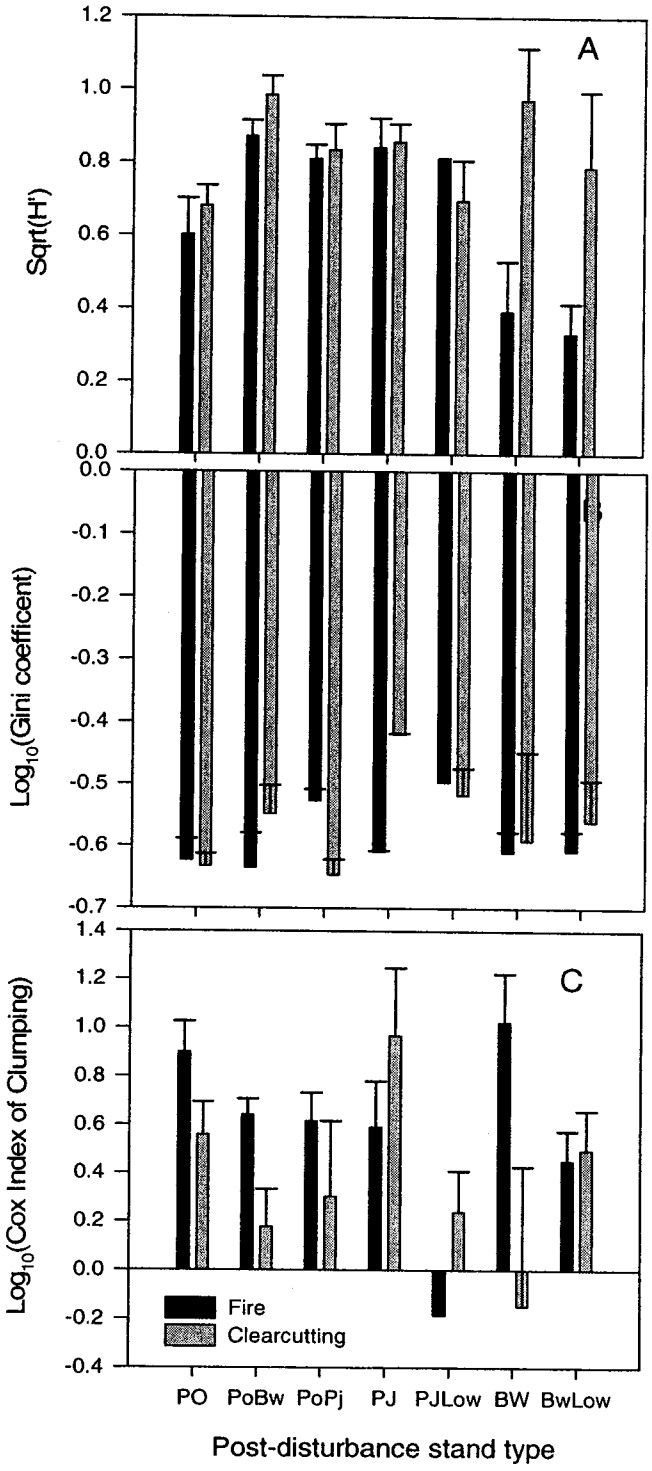

Figure 4. 3 Mean values of diversity indices in post-disturbance stand types. Transformed variables in following figures are: A – Shannon diversity index (H'), B – Gini coefficient, and C – Cox Index of Clumping. Error bars are ±1 SE.

DISCUSSION

Height growth of trembling aspen and jack pine followed the same pattern after fire and clearcutting in aspen and pine dominated stands. In aspen dominated stands, annual height growth was higher in clearcuts, while in pine dominated stands, it was higher after fire. The higher growth of aspen and pine in clearcuts in aspen dominated stands may be attributed to higher light availability, which tends to control height growth of light-demanding, shade-intolerant species (Chen, 1997; Chen and Klinka, 1998). As both aspen and pine are very shade-intolerant, the light conditions should be more favorable to these species in clearcuts where all overstory trees are removed, while in fire areas, residual live trees and standing snags provide some shade. With higher light availability, photosynthesis and in effect height growth are enhanced (Hemming, 1999).

In the PJ stand type, annual height growth of trembling aspen and jack pine was higher after fire, which is likely a result of density-dependent height growth regulation. It has been shown that response of plant height increment to increasing stand density is inverse-U shaped (Xiao and others, 2006). The initial increased height growth rate in response to increasing stand density is caused by individuals' competition for space, light and nutrients. The following decrease, however, starts when stand density becomes too high, causing a reduction in the amount of available resources. Stand density in the PJ stand type was considerably higher in fire areas compared to clearcuts (4075 trees/ha and 3100 trees/ha, respectively). The moderately higher stand density in fire areas appeared to have triggered height elongation of shade intolerant species as hypothesized

in Chen and others (1996a). Density-dependent growth also explains the higher annual height growth of trembling aspen in aspen dominated stand types where density was higher. The annual height was highest in PO stand type (density = 4555 trees/ha), followed by PoBw and PoPj (density = 3139 and 2723 trees/ha, respectively).

Height growth of paper birch was significantly higher after fire than clearcutting. Its annual height growth was twice as high in fire areas as in clearcuts. There are two possible explanations. First, since paper birch is not a commercially desirable tree species, they are often left uncut. Usually, these trees die a few years after harvesting and sprouting takes place thereafter, causing smaller height growth. Second, smaller height growth may be a result of lower nutrient levels in clearcuts. Although nitrogen content can be similar between disturbance types, available phosphorous and calcium contents have been found to be lower in clearcuts because large amounts of these elements are lost with stem removal (McRae and others, 2001). As demonstrated in fertilization studies (Safford, 1982; Van Cleve and Harrison, 1985; Safford and Czapowskyj, 1986; Van Cleve and others, 1986), paper birch is a very nutrient-sensitive species. It has been found to respond quickly with increased height growth rates to soil nitrogen, phosphorous and calcium additions. Phosphorus is a major building agent of DNA molecules and an essential element to restore energy in the form of adenosine triphosphate (ATP), while calcium is an essential element part in cell wall structure that allows transportation and retention of other elements as well as strength in plant structure (Brady and Weil, 2004).

Regeneration density of black spruce, white spruce and balsam fir was low even though these species were abundant in some pre-disturbance stands in the study area (Ilisson and Chen, 2009b). Also, their regeneration was especially sparse in burnt areas. The higher mean annual height growth of balsam fir trees after clearcutting than fire is attributed to the survival of advance regeneration (Triin Ilisson and Han Chen personal observation). Similarly, marginally higher mean annual height growth rate of black spruce in clearcuts was also partially attributed to advance regeneration of black spruce since both post-disturbance regeneration and advance regeneration were present. White spruce regeneration, however, was very low in density (average 9 trees per hectare).

Live tree structure was expected to be more diverse in clearcuts than in fire areas because of survival of advance regeneration that may increase species diversity and vertical structural diversity, and also because of the presence of compacted soil patches due to forest machinery movement that may increase horizontal structural diversity. We also expected the vertical stand structure to be more diverse in the mixed stand types because of differences in their growth rates. However, among the three studied diversity indices, only species diversity was significantly different between fire and clearcutting areas, particularly in birch dominated stand types. This is likely an effect of dominance of late-successional conifer seedlings in the pre-disturbance stands (Ilisson and Chen, 2009b). As late-successional conifers are able to grow under main canopies, there might have been abundant understory trees of black spruce and balsam fir. Fire kills understory vegetation, clearcutting, however, sustains some of it and these trees contribute to the higher observed tree species diversity.

The Gini coefficient, which characterizes tree height variation, was similarly low (0.28) after fire and clearcutting regardless of stand type. This reflects the relatively even height growth in stands that are in the stem exclusion stage and where competition for space and resources (mainly light) causes the development of canopies of even height (Chen and Popadiouk, 2002). Although there was a higher conifer proportion in clearcuts and conifers were relatively smaller compared with early successional species, the proportion was probably too small to be detected with statistical significance. An insignificant influence of disturbance type on spacing is likely attributed to compaction resistance of the sandy loam soil type and the season of the harvest. Most clearcuts in the study area were carried out when the ground was frozen which might have minimized any damage to tree roots and soil compaction.

SUMMARY

1. The results of the present study demonstrate that at the stand scale, clearcutting does not have a negative influence on tree height growth and structural diversity in trembling aspen and pine dominated stands and in mixtures of these two species. The regeneration outcome was similar following clearcutting and fire, indicating that clearcutting is an appropriate management method in terms of post-disturbance regeneration.
2. Clearcutting is potentially hazardous to the productivity of paper birch dominated stands because it significantly reduced the height growth of paper birch. The causes of reduced height growth rates need to be further investigated.

3. Clearcutting results in accelerated succession in forest types where late-successional conifers are already established in the understory. As the proportion of early successional stands in the landscape is expected to increase due to increasing fire frequency as a result of human-induced climate change (Wotton *and others*, 2003), clearcutting may be helpful in sustaining late-successional conifers in the area.

CHAPTER 5. GENERAL CONCLUSION

The purpose of this thesis was to compare fire and clearcutting effects on tree regeneration. The emphasis was on the pre-disturbance composition because of its relation to the availability and size of bud and seed banks. Below are the main conclusions including recommendations for predicting and using silvicultural treatments.

1. Stand replacing-disturbances promote broadleaves.

In the boreal mixedwoods, most broadleaf tree species are strong vegetative reproducers. This life trait allows species to occupy space considerably faster compared to species dependent on seed dispersal and "time-consuming" seedling establishment and germination. Vegetative recruits are supported by nutrients from root carbohydrate reserves of parent trees, giving an advantage in height growth and competition for space, light and other environmental resources with developing vegetation.

In boreal mixedwoods, the vegetative reproduction type (root suckering or stump sprouting) determines the regeneration abundance. Root suckering ability of *P. tremuloides* makes it an especially aggressive species after stand-replacing disturbances. Root suckering enables regeneration establishment at varying distances from parent trees, allowing species to regenerate aggressively with high sapling numbers and rapidly colonize surrounding areas. Stump sprouting of *B. papyrifera*, however, restricts the development of sprouts to the stump area of parent trees. Therefore, *B. papyrifera*

dominated stands generally have lower tree density (lower competition rate) which leaves more resources for seedlings of the same or other species.

If the goal is to sustain broadleaf dominance after disturbances, it is recommended that the areas be left for natural regeneration. However, if mixtures or conifer dominated stands are desired, species composition prior to disturbance should be considered before further silvicultural actions. Firstly, if the pre-disturbance stand is represented by even few individuals of *P. tremuloides*, it is likely that this species will dominate the post-disturbance stand. In this case poisoning or some other silvicultural method that eliminates suckers/suckering ability should be used. Secondly, the higher the proportion of B. *papyrifera* in the pre-disturbance stands the greater the likelihood that the *B. papyrifera* regeneration will suppress seed dispersing species. With low pre-disturbance proportions, regeneration abundance is expected to be fairly moderate and will likely contribute to the development of mixed stands. Decisions for additional seeding or planting should be made according to the characteristics of the specific disturbance area (availability of advance regeneration, closeness of seed source, and quality of seed beds).

2. Clearcutting accelerates succession.

There is a substantial amount of late-successional advance regeneration trees found in the clearcuts. Besides contributing to the stand composition as a late-successional accompanying species, these trees are capable distributing seeds at relatively early ages. This may lead to the development of an abundant secondary tree layer. When the stand enters to the canopy transition phase, the late-successional understory trees have an

advantage in height growth and can occupy the overstory canopy quickly when a gap is created.

For forest managers, prior to clearcutting based on their regenerating species preferences the decision should be made whether advance regeneration species are desirable in the future stand composition. If it is desirable (e.g. *P. mariana*) then focus should be on the protection of advance regeneration. However, if the advance regeneration species is less desirable (e.g. *A. balsamea*) measures to eliminate advanced regeneration should be considered.

3. Clearcutting is a justified harvesting method in *P. tremuloides* and *P. banksiana* dominated stands, but its usage in *B. papyrifera* dominated stands warrants further study.

In terms of regeneration abundance, growth rate and stand structure, clearcutting mimics the effect of fire in *P. tremuloides* and *P. banksiana* dominated stands. However, the conclusion can be made only for stands on relatively nutrient poor sandy soils and for full tree harvesting method. As there is a paucity of available literature, we presently do not know how successful *P. banksiana* regeneration would be after clearcutting in other soil types where competing vegetation may restrict establishment, or following tree-length harvesting which leaves the ground covered with cutting residues.

Clearcutting has a negative influence on the abundance and growth rate of *B. papyrifera*. The reasons behind this warrant further study. The proposed research areas

are (i) sprouting rate of live trees *versus* cut trees on the clearcuts *versus* fire killed trees, and (ii) influence of lower nutrient levels on growth rates in clearcuts compared to fire.

4. *P. mariana* does not always regenerate abundantly in the upland sites despite the fire adaptation of cone semi-serotiny.

Regeneration success is dependent on the coincidence of a number of conditions (e.g. lack of competing vegetation, mature age of pre-fire stand, sustained seed bank, suitable seed bed conditions). Therefore, in upland sites, if *P. mariana* domination is preferred following fire or clearcutting silvicultural treatments are often required (poisoning broadleaves, planting or seeding).

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APPENDIX 1.

Studies used in analysis. *Species abbreviations are given in Table 2.1.

Study	References	Disturbance	No of obser-vations	Study location	Pre-disturbance species*	Stand ages (yr)	Time since distur-bance (yr)	Sample size in original study
1	Charron and Greene, 2002	Fire	1	Saskatchewan	Pim, Pib	50-60	5	1
2	Heinselman, 1981	Fire	3	Minnesota	Abb, Bep, Pim, Pib, Pir, Pog, Pot	73-175	3	1
3	Sirois and Payette, 1991	Fire	4	Quebec	Pim	n.a	30	50
4	Chen *and others*, 2009	Fire	5	Ontario	Abb, Bep, Pig, Pim, Pib, Pot, Tho	28-175	7-9	10-20
5	Ohmann and Grigal, 1979	Fire	7	Minnesota	Abb, Acr, Bep, Pig, Pim, Pib, Pis, Pog, Pot, Qur	107-216	5	1
6	Greene *and others*, 2004	Fire	12	Quebec	Pim, Pib, Pot	63-86	2	1
7	Johnstone and Chapin, 2006	Fire	17	Yukon	Pim, Pic, Pot	25-75	19	1
8	Archambault *and others*, 1998	Clear cut	1	Quebec	Abb, Acr, Acs, Bea, Bep, Pig, Tho	n.a	20	1
9	Marquis, 1981	Clear cut	1	Pennsylvania	Prs	n.a	35	1
10	Marquis, 1967	Clear cut	1	New Hampshire	Acp, Acr, Acs, Bea, Bep, Fag, Fra, Pot, Prp	n.a	25	1
11	Roberts and Dong, 1991	Clear cut	1	Newbrunswick	Acs, Fag, Bea, Acr, Prp	n.a	2	1

12	Scholz and DeVriend, 1957	Clear cut	1	Wisconsin	Acr, Acs, Bep, Cas, Fra, Osv, Pot, Prs, Qua, Tia, Ula	n.a	5	1
13	Walker and Johnson, 1975	Clear cut	1	Alberta	Pig, Pic, Pot	84	11	1
14	Ward, 1966	Clear cut	1	Pennsylvania	Acr, Pot, Prs	55	2	1
15	Wurtz and Zasada, 2001	Clear cut	1	Alaska	Bep, Pic, Pob, Pot	150-180	27	1
16	Hughes, 1967	Clear cut	3	Ontario	Abb, Bep, Pib, Pob, Pot, Qur, Tho	n.a	7	2
17	McInnis and Roberts, 1994	Clear cut	3	Newbrunswick	Abb, Acr, Bep, Lal, Pis	n.a	3	1
18	Cooper-Ellis *and others*, 1999	Wind	1	Massachusetts	Acr, Bea, Bep, Cas, Fra, Osv, Pis, Qur	75	6	1
19	Dunn *and others*, 1983	Wind	1	Wisconsin	Abb, Acr, Acs, Bea, Bep, Fra, Frn, Osv, Pis, Qur, Tho, Tia, Tsc, Ula, Ulr	250-400	2	1
20	Foster, 1988	Wind	1	Newhampshire	Acr, Acs, Bel, Ben, Bep, Frag, Pis, Tsc	Old growth	30	1
21	Arevalo *and others*, 2000	Wind	2	Minnesota	Acn, Acr, Bep, Frn, Pib, Pir, Pis, Pog, Prp, Prs, Qua, Que, Qum, Ula	n.a	14	1

APPENDIX 2

The study plot information

Plot number	Disturbance type	Post-disturbance stand type	Time since disturbance	Regene-ration density (trees/ha)	Regeneration density by species (trees/ha)					
					Populus tremuloides	*Betula papyrifera*	*Pinus banksiana*	*Picea mariana*	*Picea glauca*	*Abies balsamea*
F1	Fire	BW	10	2350	125	2225	0	0	0	0
F2	Fire	BW	10	2500	600	1900	0	0	0	0
F3	Fire	PoPj	10	3075	2375	700	0	0	0	0
F4	Fire	BwLow	10	550	50	500	0	0	0	0
F5	Fire	BwLow	10	125	0	125	0	0	0	0
F6	Fire	BwLow	10	475	50	425	0	0	0	0
F7	Fire	PoPj	10	3350	2900	75	275	100	0	0
F8	Fire	PoPj	10	3025	1750	575	650	25	0	25
F9	Fire	PoPj	10	1725	1550	0	175	0	0	0
F10	Fire	BW	10	2275	0	1650	625	0	0	0
F11	Fire	PO	10	4525	4200	275	50	0	0	0
F12	Fire	PoPj	10	2900	1900	0	1000	0	0	0
F13	Fire	PO	10	4050	3225	25	800	0	0	0
F14	Fire	PO	10	7325	5975	600	125	75	0	550
F15	Fire	PoPj	10	2525	2400	0	50	0	0	75
F16	Fire	PO	10	3900	2875	925	0	75	25	0
F17	Fire	PoBw	10	2425	1700	625	25	0	0	75
F18	Fire	PoPj	10	2775	2600	100	25	0	25	25
F19	Fire	PoPj	10	2250	1900	0	325	25	0	0
F20	Fire	PoBw	10	3475	1750	1475	250	0	0	0
F21	Fire	BW	10	1600	0	1600	0	0	0	0
F22	Fire	BwLow	10	50	0	0	0	0	50	0
F23	Fire	PO	10	3350	3350	0	0	0	0	0

F24	Fire	BW	10	2875	0	2775	100	0	0	0
F25	Fire	PoBw	10	2225	1500	725	0	0	0	0
F26	Fire	BwLow	10	950	0	950	0	0	0	0
F27	Fire	BwLow	10	1225	75	1150	0	0	0	0
F28	Fire	BW	10	2325	0	2325	0	0	0	0
F29	Fire	BwLow	10	625	0	625	0	0	0	0
F30	Fire	BwLow	10	1050	0	1050	0	0	0	0
F31	Fire	PoPj	10	4150	2375	375	1275	125	0	0
F32	Fire	PO	10	3850	3550	25	225	50	0	0
F33	Fire	PoPj	10	3750	2050	50	1600	50	0	0
F34	Fire	PjLow	10	1250	0	175	1000	50	25	0
F35	Fire	PoPj	10	2750	1375	0	1250	125	0	0
F36	Fire	PoPj	10	1950	1050	0	775	125	0	0
F37	Fire	PoPj	10	1825	1175	100	550	0	0	0
F38	Fire	BwLow	10	200	0	150	0	0	50	0
F39	Fire	BwLow	10	925	125	800	0	0	0	0
F40	Fire	BwLow	10	900	0	900	0	0	0	0
F41	Fire	PJ	10	4125	975	425	2725	0	0	0
F42	Fire	PJ	10	4025	75	675	3250	25	0	0
F43	Fire	BwLow	10	700	175	500	0	0	0	25
F44	Fire	BwLow	10	375	0	375	0	0	0	0
F45	Fire	BwLow	10	150	100	50	0	0	0	0
F46	Fire	BwLow	10	700	0	700	0	0	0	0
F47	Fire	BwLow	10	1025	0	1025	0	0	0	0
F48	Fire	BwLow	10	275	100	175	0	0	0	0
F49	Fire	BwLow	10	300	0	275	0	0	0	25
F50	Fire	PoPj	10	2525	1450	350	700	25	0	0
F51	Fire	PoPj	10	3200	2250	25	900	0	0	25
F52	Fire	PO	10	4425	3150	150	1125	0	0	0
F53	Fire	PO	10	5100	4850	0	175	50	0	25
F54	Fire	PoPj	10	2475	1000	0	1475	0	0	0
F55	Fire	PoPj	10	3075	2175	25	850	25	0	0
F56	Fire	PoPj	10	2575	1450	0	1050	75	0	0

L1	Clearcutting	PO	11	4550	3975	125	0	0	0	450
L2	Clearcutting	PO	11	3550	3375	50	0	0	0	125
L3	Clearcutting	PO	8	3825	3775	50	0	0	0	0
L4	Clearcutting	PoBw	8	3375	1625	1650	0	0	75	25
L5	Clearcutting	PO	8	3900	3600	250	0	0	0	50
L6	Clearcutting	PoPj	9	2025	1525	150	0	225	0	125
L7	Clearcutting	PO	11	4150	3300	225	75	25	50	475
L8	Clearcutting	PO	11	4475	3675	625	100	50	0	25
L9	Clearcutting	PoPj	11	1250	1175	0	0	0	0	75
L10	Clearcutting	PO	11	4725	3500	950	75	25	0	175
L11	Clearcutting	PoBw	8	3750	1275	950	0	125	0	1400
L12	Clearcutting	PO	11	3700	2850	425	0	25	0	400
L13	Clearcutting	PO	9	5625	4000	575	1025	25	0	0
L14	Clearcutting	PO	8	5475	3850	875	750	0	0	0
L15	Clearcutting	PoBw	8	2075	1075	1000	0	0	0	0
L16	Clearcutting	PoPj	8	2975	2550	275	0	50	0	100
L17	Clearcutting	BwLow	8	1475	25	675	0	175	150	450
L18	Clearcutting	BwLow	8	1225	0	1200	0	0	0	25
L19	Clearcutting	PJ	8	3100	50	0	2500	525	0	25
L20	Clearcutting	PjLow	8	650	0	0	450	150	0	50
L21	Clearcutting	BwLow	8	50	0	0	0	50	0	0
L22	Clearcutting	PoPj	8	2750	1900	475	350	0	0	25
L23	Clearcutting	PoPj	8	2450	2025	100	275	0	0	50
L24	Clearcutting	PO	8	3525	3400	0	25	75	0	25
L25	Clearcutting	PoPj	8	3625	2375	625	50	150	50	375
L26	Clearcutting	BwLow	8	1075	625	75	375	0	0	0
L27	Clearcutting	PjLow	10	975	0	0	925	50	0	0
L28	Clearcutting	PjLow	10	1725	50	0	1600	75	0	0
L29	Clearcutting	PjLow	10	1525	0	0	1525	0	0	0
L30	Clearcutting	PjLow	10	700	50	0	350	125	25	150
L31	Clearcutting	PjLow	10	850	0	0	775	75	0	0
L32	Clearcutting	PjLow	10	975	0	0	900	75	0	0
L33	Clearcutting	PoBw	8	3900	2225	1575	0	25	0	75

L34	Clearcutting	BwLow	8	1775	625	425	175	475	25	50
L35	Clearcutting	PjLow	8	1750	0	575	625	550	0	0
L36	Clearcutting	PoPj	8	3100	2100	375	75	525	0	25
L37	Clearcutting	PoBw	8	3625	1875	1325	275	150	0	0
L38	Clearcutting	BwLow	8	1350	450	175	275	450	0	0
L39	Clearcutting	PO	8	3900	3100	500	25	250	0	25
L40	Clearcutting	PoBw	8	3400	1275	1200	100	450	0	375
L41	Clearcutting	BW	14	2725	175	2225	0	225	25	75
L42	Clearcutting	BW	8	2425	375	1275	550	150	0	75
L43	Clearcutting	PJ	8	3100	50	500	2250	300	0	0
L44	Clearcutting	PjLow	8	1100	50	0	550	500	0	0
L45	Clearcutting	PjLow	8	725	25	0	400	300	0	0
L46	Clearcutting	PO	8	6600	6000	325	225	25	25	0
L47	Clearcutting	PO	8	5675	5350	75	25	175	0	50